ON THE ECOLOGICAL NICHE AND NOCTURNAL ACTIVITY OF THE AYE-AYE (Daubentonia madagascariensis)(Dissertation_全文)

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AN ECOLOGICAL AND BEHAVIORAL STUDY OF THE AYE-AYE (Daubentonia madagascariensis)

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ABSTRACT

This report forms one of a series of papers examining my new hypothesis regarding the ecological niche of the aye-aye (Daubentonia madagascariensis): I proposed a hypothesis that aye-ayes's unusual adaptations are more reasonably explained by hard-nuts feeding rather than by wood-boring insect larvae eating.

According to our extensive survey, distribution of the aye-aye and those of Canarium spp. (which bore hard-nuts) overlapped in the eastern coast and in the central highland of Madagascar.

I observed aye-ayes at the Nosy Mangabe Special Reserve over 33 nights in total (2,910 units when an observation of 1 minute duration is taken as a unit) at three different periods; i.e., December 1988, June to July 1989 and September to October 1989. I observed aye-ayes eating ramy nuts (Canarium spp.) throughout the entire observation period, the bark (abnormal outgrowth of the cambial layer) of Afzelia bijuga from June to July and September to October, and insect larvae, beans of Entada phaseoloides and nectar of Macaranga cuspidata from September to October.

The aye-aye spends a relatively high proportion of time engaged in feeding activity (over 40%) during October and December when ramy forms the main diet while from June to July, and September when other food items are additionally consumed, the proportion of resting time becomes relatively high (over 10%).

Although aye-ayes were often spotted singly, it was also common to see

throughout the observation periods more than one individual (four at maximum) active adjacent to each other (13% of all the observation units at which the aye-aye was spotted).

Two species of ramy (Canarium spp.) are distributed in the Nosy Mangabe Special Reserve, and C. Boivini was found to bear fruits over the entire observation period. A single nut of the ramy provides 4.38Kcal of energy and requires 2 minutes on average for consumption. I estimated the energy intake as 262.8 kcal that an aye-aye gained overnight.

KEY WORDS: Aye-aye, Daubentonia madagascariensis, Feeding behavior, Canarium spp., Afzelia bijuga, Hard-nut adaptation hypothesis.

INTRODUCTION

When the aye-aye was discovered, no ecological observations were reported because, as was described by Sandwith in the letter to Owen (Owen, 1863), the researchers could not gather information on the aye-aye's ecology from native inhabitants who often believed that the animal (called "hai-hai" by local people) was incarnation of "fady" (evil spirit). From our survey it was also confirmed that, except for the northern area of the central highland, Mandritsara and Befandriana Nord where the people have recently become accustomed to eating aye-ayes, aye-ayes have been regarded to date as taboo and prohibited to eat in districts on the east coast such as Maroantsetra, Antalaha and Mananala. It is said that whenever a local inhabitant in those districts sees an aye-aye in the daytime he kills it because it is supposed to bring misfortune. Thus, it is still difficult to gather information on the living state of aye-ayes from local people. A field survey on the aye-aye was launched by Petter et al. in 1957 (Petter and Petter-Rousseax, 1959; Petter and Peyrieras, 1970; Petter, 1977; Petter et al., 1977), but their survey covered all prosimian groups and was not restricted to the aye-aye. The aye-

aye's nocturnal activity and the scant information available from local inhabitants have severely retarded study of the aye-aye.

Less than 10 studies on the aye-aye were reported during the 1980s, including our own, and most were only fragmentary (Bomford, 1981; Kemf, 1983; Constable et al., 1985; Pollock et al., 1985; Ganzhorn and Rabesoa, 1986; O'Connor et al., 1987; Iwano and Iwakawa, 1988; Wilson et al., 1989). The data, in short, consisted only of information regarding the location of aye-aye observations.

Iwano and Iwakawa (1988) reported for the first time that the aye-aye feeds on nuts of ramy (Canarium spp.), a plant indigenous to Madagascar. Based on this finding, we proposed an alteration of the previously advocated woodpecker hypothesis (Cartmill, 1974) regarding the ecological niche of the aye-aye. The woodpecker hypothesis related to the unusual morphological characteristics of the aye-aye and its feeding behavior. The combined function of its continuously growing chisel-like incisors and its narrowed third digit have drawn the attention of many workers since its discovery. Cartmill (1974) suggested that these two peculiar morphological traits represented an adaptation for the extraction of wood-boring insect larvae. This permits the aye-aye to fill the ecological niche normally filled by woodpeckers, which are absent form Madagascar.

Our new hypothesis is based on the following three points: (1) The continuously growing incisors and the slender third digit of the aye-aye are an indispensable tool, suitably adapted for feeding on ramy nuts in a very efficient way. (2) The aye-aye is exceptionally large (3 kg) compared with other insectivorous primates (0.06-0.2 kg) and it is unlikely that it could depend upon insects as a major food source. (3) There are two kinds of birds preying on wood-boring insect larvae on Madagascar (Petter, 1977). Accordingly, the ecological niche of feeding on wood-boring insect larvae is

not completely open. On the other hand, the niche of feeders on hard-nuts is unoccupied by animals other than the aye-aye, since squirrels are absent from Madagascar (Petter, 1972).

The hypothesis suggests a number of questions: How is the ramy distributed in Madagascar? How do the distributions of the ramy and the aye-aye overlap? Is the ramy nut truly the staple food of the aye-aye? When does the ramy bear fruits in the area where the aye-aye lives? What does the aye-aye eat when the ramy does not bear fruits?

This study was undertaken with the aim of searching for answers to these questions by revealing the ecology of the aye-aye, and to test the validity of hard-nut adaptation hypothesis.

METHODS

The survey on the distribution was carried out in the forested district of the eastern coast and the northern district of the central highland of Madagascar in November to December 1988 and August 1989. In the survey, we selected several study sites between 15°29' S and 25°S, to get a general view of the distribution of the aye-aye and the ramy in question.

The study concerned with the ecology of the aye-aye was conducted at the Nosy Mangabe Special Reserve including a survey on the seasonal changes in fruiting of the ramy (Canarium spp.). The ecological study of the aye-aye was conducted in December 1988, from June to July 1989 and from September to October 1989. The phenological study on the fruiting of the ramy was conducted between June 1989 and June 1990.

The research team, consisting of two to six members, walked tracks in the mountainous region along the southwest coast of Nosy Mangabe, and along the beach alternately every night (from 18:00 hrs till 5:00 hrs the next day), and followed the aye-aye spotted during survey to continue observation.

Throughout the survey we used a beam light of 150,000 lux (12V) and torches (3-6V).

The observation period at night was divided into units of 1 minute duration and every activity of the aye-aye was allotted to an appropriate unit. The items selected for description were as follows.

(1) Activity: feeding, moving, resting, grooming, vocalization, and social behavior.

(a) Feeding:

It was often difficult to directly observe aye-ayes putting something into the mouth to eat because observations were made while aye-ayes were feeding under a thicket of tree-tops about 20m overhead the observers for ramy or, while the aye-ayes faced tree-trunks with their backs toward the observers for Afzelia bijuga. However, I could confirm aye-ayes' eating through a number of indirect methods: the aye-aye generates rather loud, characteristic sounds in association with gnawing the shell (for ramy nuts), and torn fragments create sounds upon falling (both for ramy and A. bijuga). Although it is actually a preparatory activity, peeling off the pulp and the bark during ramy and A. bijuga feeding was scored under the category of feeding, because the aye-aye's feeding process including peeling, gnawing out a hole and putting the contents into the mouth proceeds continuously without notable demarcations. Furthermore peeling forms a characteristic feeding method of the aye-aye.

(b) Moving: When the aye-aye was observed to move.

(c) Resting: When the aye-aye was observed to be immobile.

(d) Grooming: When the aye-aye was observed to rub its body with its mouth, hands or feet or lick it by tongue.

(e) Vocalization: When aye-aye voices were heard, they were noted separately

from other behaviors, and, if possible, the number of voices was also noted. Whether or not the voice was generated by an individual under observation was noted under the heading of "Other remarks". I could discern the voice of aye-ayes based on two kinds of characteristic voicing.

(f) Social behavior: When more than one individual were observed to be engaged in interactions such as charging or chasing, etc. More than one individuals only sitting side by side without apparent interaction was not treated as social behavior.

(2) Foods: name and parts eaten.

(3) Number of fallen ramy nuts.

(4) Other remarks: Place (tree trunk, branch, crown and ground), height (over 25m, between 25 and 10m, and less than 10m).

The survey on seasonal changes of fruiting of ramy consisted of two parts: one was to study fruiting of the trees sampled (46 for C. madagascariense and 1 for C. Boivini) twice monthly, and the other, to count the total number of ramy trees with fruits within the study area.

STUDY SITE

In the survey on the distribution of the aye-aye and ramy, we selected several study sites between Maroantsetra (15°29' S) and Tolanaro (25°S) in the eastern coast and around Befandriana Nord (15°15' S) in the northern part of the central highland (Fig.1).

I selected Nosy Mangabe Special Reserve for the ecological study of the aye-aye. Nosy Mangabe (15°29'S and 49°45'E, 520 ha and 331 m above sea level at its highest point) is a small island uninhabited by people located in the deepest corner of Antongil Bay on the eastern coast of Madagascar. Its entire area was designated as a special reserve in 1966 and nine aye-ayes were released on the island in 1967 (Petter, 1977).

A description of its vegetation has already been given elsewhere (Iwano and Iwakawa, 1988). Two species of ramy grow in Nosy Mangabe, C. Boivini from the coast to over 200m above sea level and C. madagascariense in areas over 100m above sea level. Thus, C. Boivini appears to be the dominant species in Nosy Mangabe. A. bijuga grows from the coast to less than 75m high above sea level. I chose two study sites along the western coast of the island (Fig. 2).

The land around Antongil Bay mainly consists of granite cliffs more than 150 m high (Battistini, 1972). The Nosy Mangabe island is also composed of granite and has steep slopes around it.

The weather of Maroantsetra has never been officially observed. Thus, the average monthly temperature in the region should be taken to be the average of the data at Toamasina (18°9'S) and Vohemar (13°22'S) (from Fig. 2 in Donque, 1972), indicating that the maximum average temperature (26°C) is in February and the minimum (22.5°C) falls in July to August with only a 3.5°C difference between the two.

The region near Antongil Bay receives the most precipitation in Madagascar, or 350mm per month on average (Donque, 1972). The rainy season starts in December and continues until March. Even after April, however, the region often receives heavy rains through to July. The region is comparatively free from rain from August to November.

At Nosy Mangabe Special Reserve, the average monthly temperature was lowest in June, which is partly explained by the fact that observations began from the latter half of that month (Table I). The daily weather was entered only as a reference because the weather changed so drastically that it was practically impossible to include it under a single headline.

RESULTS

1. Distribution

The data obtained concerning existence of the aye-aye in eastern coast can be summarized as follows: aye-ayes themselves were observed at Nosy Mangabe, Andasibe, and Ranomafana; tooth marks on Afzelia bijuga trees and three nests were found in Maroantsetra; feeding tracks on ramy nuts were seen in Tolongoina, and Anosy hills. In these places, we could find two species of the ramy (C. Boivini and C. madagascariense).

In the central highland, we confirmed existence of the aye-aye at Befandriana Nord by the substantial evidence (tooth-marks, feeding tracks on ramy nuts, and five nests). Mr. H. Fukazawa collected a tail of aye-aye which had been eaten by local people at Mandritsara. In these districts, there were forests dominated ramy (C. madagascariense) and mango trees along the rivers.

The ramy flourishing at Befandriana Nord is called "haramy", and its fruiting season has been said to fall between March and May. However, we saw that they bore fruits even in August .

2. Diet

The diet of the aye-aye was confirmed to include five kinds of plants (including two kinds of Canarium genus), and a number of wood boring larvae, though their genera could not be identified (Table II).

Aye-aye's feeding sequence on ramy nut consisted of four steps: (1) searching for a fruit item; (2) holding a fruit and settling down; (3) scraping of the pulp and gnawing into the hard shell of the nut, and (4) extracting and eating the contents.

Aye-ayes ate the interior of the bark or the cambial layer of A. bijuga (provisionally referred to as "bark" hereafter) while conducting the survey from June to July, and from September to October. When feeding on A. bijuga, the aye-aye peels off the bark and eats the underlying cambial layer releasing a sweet odor by scooping it out with the lower incisors (Fig. 3).

I observed aye-ayes feeding on Macaranga cuspidata and Entada phaseoloides. For the former, it is likely that aye-ayes eat the nectar or pollen of its flowers, and they feed on the large beans of the latter.

In each survey periods, I confirmed feeding marks on dead trees throughout the study area, possibly left by aye-ayes searching for wood boring larvae. In the survey lasting from September to October, I observed aye-ayes eating larvae after tearing open the bark of a branch with their teeth.

Seasonal changes of diet

I confirmed feeding on ramy nuts by aye-ayes throughout the survey periods, and, although I did not directly observe aye-ayes feeding on ramy nuts from June to July 1989, I could detect new feeding marks on ramy nut shells. This period coincided with a time when aye-ayes mainly consumed A. bijuga. In the survey from September to October, I could not observe directly aye-ayes feeding on ramy until late September. Macaranga cuspidata and Entada phaseoloides were observed only in September and October as diet of the aye-aye. Although the changes of aye-aye's diet were so drastic, these appearance might be mainly because of the fragmental nature of my data. Therefore, more detailed observation is needed for the seasonal changes of their diet.

3. Feeding Behavior

Feeding records for individual food items were summed for each hour of the periods when aye-ayes' activity was observed (Table III). Aye-aye's feeding time varies depending on the food item eaten. A. bijuga was eaten most frequently between 18:00 and 22:00 hrs (91% of the total observation units at which A. bijuga was found to be eaten), feeding on ramy occurred most often between 22:00 and 0:00 hrs (72.5%), and eating of E. phaseoloides beans and insect larvae took place before 22:00 hrs.

The longest feeding time span for ramy was 111 minutes with an average of 59 minutes (S.D.=32.0, N=12). Feeding times for A. bijuga ranked second in

duration, the longest time being 60 minutes. The average duration was 29.4 minutes (S.D.=25.3, N=14). For the calculation of the average, I excluded those cases in which feeding on A. bijuga lasted for less than 1 minute.

Feeding on the flowers of M. cuspidata was observed four times with the longest duration being 22 minutes. Feeding on insect larvae was observed four times with the longest duration being 9 minutes. I observed aye-ayes feeding on the beans of M. cuspidata only once with a duration of 1 minute.

I could deduce the rate at which an aye-aye ate ramy nuts from the sounds generated by falling nuts discarded by the aye-aye engaged in feeding, and had 11 opportunities for such measurements (total duration being 496 minutes). That the time an aye-aye requires for consuming a ramy nut is 126 seconds on average (S.D.=0.5, N=11). This value is slightly longer than the equivalents in the previous study conducted in December 1984 (102 seconds), or under artificial feeding conditions (103 seconds, Iwano in press), because the value in the present study includes searching time. Taking all things together, it can be said that the aye-aye consumes about one ramy nut every 2 minutes under natural conditions.

4. Hourly Changes of Activity and Duration of Individual Activities

To observe the nocturnal activity of aye-ayes, I waited at a place where a main food item of the season was present; spotting and following aye-ayes from there (Fig. 4).

In June, July, September and October 1989, aye-ayes appeared in A. bijuga trees along the coast in the evening, fed in the trees, and moved toward the mountainous region. It frequently occurred that aye-ayes, after moving a while, disappeared suddenly, which was probably because they were hidden in their nests or resting places. In fact, on October 3, 1989 I could observe an aye-aye, after moving, entering its nest.

This movement sometimes took place through the same routes. This suggests that an individual, after feeding at a frequented feeding site, returns to its resting place.

In general, aye-ayes used higher tree tops over 20m above the ground for moving, but they occasionally descended to a height of 2 to 3m above the ground, which was close to the observers. It remains unclear whether these acts represented displays of threat or mere curiosity.

Aye-ayes move about by a variety of methods including: traversing branches by holding onto twigs, swinging from branch to branch by holding onto the tips of branches (sometimes the animals move upside down hanging by their limbs), climbing up or down tree-trunks using their claws, jumping from one branch to another, and sliding down a vine by hanging from their forelimbs (witnessed only once when tried by a young individual). During the moving, aye-ayes did not use their third digits for handling and grasping the branches and the trunks. Movement on the ground was never observed.

A total of 2,910 observation units were scored, of which 35.2% comprised feeding activity (Table IV). Feeding activity was comparatively high in October and December, while resting showed a decrease in those months (test of the difference between two proportions; See Appendix I).

4. Social Relations

1) Observation of more than one individuals being active in close proximity.

In general, aye-ayes were observed singly, separated from other individuals. However, throughout all study periods, more than one aye-ayes (4 at maximum) were frequently observed to be active adjacent to each other (Table V). "Adjacent" means a distance which permits an observer to identify the individuals concerned at the same time, and is typically less than 20 m, except when the individuals vocalize. Of course, it is certain that aye-ayes

can perceive other members from further than 20 m.

Close proximity of two members was observed for a total of 240 minutes or 8.3% of all periods during which aye-ayes were observed to be active (2910 minutes). Accordingly, the data on social activity totaled 12 minutes in duration, or about one twentieth of the periods at which proximity of two members was confirmed. The duration at which more than three individuals were observed in the same place was 137 minutes (4.7%). Thus, more than one aye-ayes were active close to each other in about 13% of all the periods during which aye-aye activity was observed.

The duration for which more than one aye-ayes were observed in the same place became shorter from June to July, which may be explained by the generally lowered activity of aye-ayes at that time.

In December (1988) and from June to July (1989), more than one aye-ayes (4 at maximum) was observed to feed on ramy or move within a distance of 20m to each other. In those periods, however, even though aye-ayes approached to within a distance of 3 to 4m to each other, they soon moved apart without displaying any notable social interaction during such contacts.

2) Social behavior

From September to October (1989), contacts between different individuals occurred on 16 occasions and of them eight were associated with social behavior.

The social behavior observed during an encounter can be roughly classified into aggression over feeding places and interactions resembling courtship.

(a) **Aggression over feeding places**

Aggression over feeding places was observed twice on September 25 and September 29. The former case concerned a young female feeding on an A. bijuga tree which quarreled three times with another female approaching her,

finally chasing away the challenger. Immediately after the row, the young female resumed feeding on the bark of the same A. bijuga despite the opponent's presence only 6m away. In the latter case, a young male was eating ramy when another individual (sex unknown) approached, only to be chased away. There were a number of vocalizations consisting of high-pitched "Kwee-a" sound between the male and the approaching individual.

(b) **Other interactions**

Interactions suggestive of courtship were observed six times, of which three consisted of a series of actions involving four different individuals, two consisted of a female approaching a male and chasing after him (for five minutes in one case, and 33 minutes in the other), and in one case, same two individuals were perched in a tree.

For examples, at 20:05 hrs on September 20, a young male was feeding on a A. bijuga, when a young female with blind left eye approached. The two approached suddenly, and immediately parted. The two repeated sudden approach followed by immediate parting at 20:09 and 20:12 hrs. They did not use hands nor bite each other. I could not determine which one was dominant to the other. During these activities they remained within a distance of 3m to each other. Later the two moved slowly keeping a distance of less than 10m to each other.

The same young male and female were perched in a tree of M. cuspidata 6m apart from each other. The male left for a while, returned to the young female at 20:21 hrs, and, after making a quick approach, stayed away from her. At 20:34 hrs, the young male left the female, who was now resting. Later, the female intermittently moved and rested. In the meantime, voices having a "Kwee-a" sound were heard six times up till 21:23 hrs from a place 15-30m away. However, the female remained unresponsive to them.

At 21:23 hrs, a young male (it was unclear whether this was the same individual as above) appeared anew. At 21:25 hrs, the male circled round the female at a distance of 4m, and then approached her to a distance of 1m. At 21:32 hrs, the male followed the female, who was now moving, at a distance of 4-6m from her. At 21:44 hrs, the two were observed resting at a distance of 4m from each other. At 21:48 hrs, the female was observed to be absent and the male began to eat M. cuspidata flowers .

The next example also concerns the female with the blind left eye and a young male.

At 0:54 hrs on October 4, while the female was engaged in feeding on ramy, a young male approached, rested at a distance of 10m from her and engaged in self-grooming. At 0:58 hrs, the two vocalized, and then the female attacked quickly and retreated. Later, the two rested until 1:02 hrs at a distance of 1.5-3m from each other. They disappeared for awhile, but their calls were heard 12 times between 1:12 and 1:25 hrs. They appeared again and attacked together at 1:27 hrs again at 1:28 hrs. At 1:34 hrs, the female started to move away, and soon thereafter the male also moved off, and they disappeared.

3) Vocalization

Throughout all seasons, aye-ayes generate high-pitched calls sounding like "Nee-a", and they exchange these calls with each other (Fig. 5). This call has a frequency of 3KHz and is 80msec in duration (analyzed by Dr. N. Masataka using a digital sonagraph 7800, KAY Electronics Co.).

This call corresponds to the one Petter (1977) described as a "cree" sound, which was exchanged between a mother and its baby in the wild. Petter and Charles-Dominique (1979) did not mention this wave form.

These vocalizations could be heard in various situations, and, in particular, were frequently heard in December 1988. At that time, a young

individual, emitting such calls repeatedly, turned round and round the same ramy tree. From 8:00 to 9:00 hrs on December 19, the interval of repeated calls was 9-16 seconds. At 1:00 hrs on December 20, the same individual (so assumed), which had continuously emitted the calls, encountered another bigger individual, but they soon left each other. During this period, aye-ayes were not observed to feed on ramy. Probably in this case, the calls were exchanged between the young animal and its parent, while in the cases described above (occurring from September to October 1989), male-female pairs communicated with each other by vocalizing.

A second kind of vocalization was heard under certain relations with the observers. On July 1, when a young female was feeding on the bark of the No. 2 A. bijuga tree along the coast, an adult male appeared on the No. 1 A. bijuga tree (about 20m apart from No. 2) and emitted a low, resonating "Kuftt, kuftt" sounding, probably as a threat to the observers. This individual repeated the same call and moved into the forest, while the female continued eating the bark as before. At 21:30 hrs on July 3, a young male appearing on a No. 1 A. bijuga tree vocalized in the same way toward the observers.

6. On The Ramy Nuts

1) Seasonal changes in the fruiting of ramy

I undertook surveys on the distribution of ramy and its fruiting in study areas A in December 1988 and June 1989 (Fig.6).

In December, I studied 185 ramy trees in study area A, and found that 41 (22.2%) bore fruits, and in June found that 16 of 281 ramy trees (5.7%) bore fruits, one of which was C. madagascariense. I studied 23 ramy trees in study area B in September, and found that five (21.7%) developed fruits. In addition, I could confirm that at least three of the ramy trees that had bore fruits in December were still in fruiting in June of the next year.

For further confirmation of this point I launched a survey from June 1989 to October 1990 in which 47 ramy trees, including one C. madagascariense, were sampled and marked to follow their fruiting twice monthly (Appendix II). According to our survey, the fruiting season of C. Boivini started in January and lasted until October (Table VI). In November, December and January, its blossoms were observed.

The one C. madagascariense chosen as a study subject displayed many fruits from January to August. I could see only two nuts in September, indicating that it practically ceased to bear fruits. Its fruiting season was similar to C. Boivini.

Contrary to the result of my phenological survey, in December 1984 and 1988 I observed many ramy fruits in those sample trees. Therefore, we can say that C. Boivini bears fruits all the year round in Nosy Mangabe.

2) Nutritional analysis of ramy nuts

Nutritional analysis of the edible portion of a ramy nut revealed that it contains a high fraction of lipids and has a high energy content (584Kcal/100g) (Table VII. Analyzed by Japan Food Analysis Center). The conversion factors for calories were 3.47 for protein, 8.37 for lipid and 4.07 for carbohydrate. This nutritional composition and energy content is equal to the walnut, the roasted content of which has an energy of 673Kcal/100g (Resources Council, Science and Technology Agency, Japan, 1985).

The edible portion of a ramy nut weighs about 0.75g which corresponds to 4.38Kcal in terms of energy.

DISCUSSION

1. Correlation between Distribution of the Aye-aye and that of Ramy

Distribution of the aye-aye and those of Canarium spp. overlapped in the eastern coast and in the central highland of Madagascar. In the eastern

coastal region two species of ramy coexist with different fruiting seasons. C. Boivini has fruits in almost all season, while C. madagascariense has fruiting season between May and September (Cabanis et al., 1970). Thus it can be said that the tropical forest in the eastern coastal region would be advantageous for the aye-aye to utilize ramy nuts as a staple food.

Of the ramy (genus, Canarium; family, Burseraceae) three species are known in Madagascar. The distribution of the third species, C. pulchrebracteatum Guill, which occurs in the south-western part (Perrier, 1946), is a topic for future study, since an extinct giant aye-aye (D. robusta) was distributed in similar locality (Lamberton, 1934; MacPhee and Raholimavo, 1988).

2. Food Selection by Aye-Ayes

In 1985, Pollock et al. reported that aye-ayes' feed on the bark of A. bijuga trees. From their findings of bark deformed by parasitism, bitten off by aye-ayes, these investigators suggested either that aye-ayes consume the sap from the tree, or feed on insect larvae and frogs inhabiting the bark. According to our observations, however, aye-ayes did not eat insect larvae nor frogs in the bark of A. bijuga trees but preferentially feed on the fragrant parts of the cambial layer beneath the parasitically induced outgrowths of A. bijuga bark.

The feeding habits of aye-ayes are characterized by the fact that they ignore plant shoots and foliage, or other important food items of the prosimian groups living in the same area.

Whether the aye-aye can subsist solely on the bark of A. bijuga is a question to be dealt with in the future. For A. bijuga to sufficiently nourish the aye-aye it is necessary that its bark has sufficient energy content. The facts that the aye-aye feeds only on the bark deformed by

parasitism and not on the intact bark, and that A. bijuga trees are only distributed along the coastal region, suggest that A. bijuga bark forms a supplementary food item peculiar to the coastal region.

3. Can Ramy Sufficiently Nourish the Aye-Aye?

In the ecological survey continued with some interruptions from December 1988 until September/October 1989, I found that aye-ayes largely depended on ramy, supporting our hypothesis that the ramy forms the staple food of the aye-aye. But it remains to be determined whether the aye-aye can actually subsist on ramy nuts alone.

1) Estimation from the energy content of the ramy nut

The energy contained in the albumen of a ramy nut the aye-aye habitually eats is rather high at 584 kcal/100g. As the content of one ramy nut is 0.75 g, a ramy nut has a total energy of 4.38 kcal on average. The quantity of nuts an aye-aye takes over a night can only be guessed at, but, provided that an aye-aye is engaged in feeding for about two hours a night (this may be a rather low estimate, because more than 31.1 percent of active record in the night, about 3 hours, was calculated as feeding) consuming one nut every 2 minutes, it consumes 60 nuts overnight, resulting in a total energy intake of 262.8 kcal. Since a macaque weighing 4.2 kg has been estimated to have a basal metabolic rate of 207 kcal (Benedict, 1938 cited in Kleiber, 1975), the above figure appears to be sufficient for sustaining an aye-aye with a weight of about 3 kg, and the aye-aye may have a comparatively low metabolic rate because it belongs to prosimian groups (Müller, 1985).

In the survey carried out in December 1984, I found that aye-ayes continuously fed on ramy nuts for almost three and a half hours on end, resulting in ingestion of a total energy of 459.9 kcal. This allows aye-ayes to enjoy a high energy intake during seasons of ramy nuts abundance. In such periods, the aye-aye can build up fat deposits within the body, but it remains

to be confirmed whether this fat is sufficient to sustain the aye-aye through other periods lasting almost half a year when ramy nuts become less available. This answer awaits a detailed nutritional study.

(2) Estimation of the aye-aye's population at the Nosy Mangabe Special Reserve

The ramy trees in the study area have an average diameter of 107.7 cm at human breast height (N=23; S.D., 42.7; range, 45.0-166.0cm). While some trees have larger diameters, their buttress roots are so well-developed that it was difficult to measure the diameter. These trees reach a height of over 20m, making it difficult precisely to estimate how many fruits such a tree bears annually on average. As a trial, however, an estimation was made on a tree (No. 15, 14.5cm diameter at human chest height), which gave 3,000 as an estimation of average fruits produced by one tree over a year. Provided that the aye-aye consumes 60 ramy nuts overnight from the above observation, one ramy tree can provide 50 day-rations. The study area A (about 20ha) has a total of 281 ramy trees within its confines, and the ramy trees bearing fruits in December amounted to 22.2% of the sample examined (185), which, when taken as a fraction of the total, corresponds to 62.3 trees. These trees produce 3,115 day rations, which, when divided by 365 (days per year), gives 8.53 as the number of aye-ayes that can be sustained by those trees in study area A. These figures give 2.34 ha (20 ha / 8.5 individuals) as an activity area per aye-aye, which corresponds to a density of 42.7/km^2. When this density is extended to the whole area of the Nosy Mangabe Special Reserve having an area of 5.2 km^2, the value of 222.2 is obtained as the total population of the aye-ayes which can be sustained by the Nosy Mangabe area.

There are, in addition, a number of factors limiting the aye-aye's population: the Nosy Mangabe area also serves as the habitat for Varecia

variegata variegata and Lemur fulvus albifrons which are in a competitive position with aye-ayes for ramy nuts (Iwano, 1989). Furthermore, ramy nuts are not available throughout the year, and ramy nuts are not evenly distributed over the whole area. This issue would be different if aye-ayes could store ramy nuts in some way or another. In fact, the aye-aye in captivity at Botanical and Zoological Park in Tsimbazaza was observed to deposit coconuts in a secret cache. In short, from the nutritional standpoint, the above figures suggest that the Nosy Mangabe Special Reserve has ample capacity for keeping a considerable number of aye-ayes alive (the energy balance at periods when ramy fruits are comparatively scarce is ignored for purposes of this discussion).

Future discussions of aye-aye ecology should be facilitated by using such figures as references, especially when considering activity areas of aye-ayes and their population density.

4. Can Wood-Boring Insect Larvae Sufficiently Nourish Aye-Ayes?

In feeding on the bark of A. bijuga and insect larvae, as already noted by Petter (1977), it is unlikely that the energy expended in feeding can be made up for by the energy actually ingested. Aye-ayes, however, seemed to feed on insect larvae throughout the survey periods as judged from feeding marks left by aye-ayes.

In June 1986, I identified one tooth mark left on the surface of a dead tree in isolation. To reach that tree the aye-aye must have walked on the ground, an unusual behavior for this arboreal creature. This indicates a remarkably intense predilection of aye-ayes toward wood-boring larvae. Such favorite food articles would be eaten throughout the year; that is, whenever available, aye-ayes feed on them at will.

The observation units during which aye-ayes were observed to feed on

wood-boring larvae accounted for only 1.4% of all observation units related with feeding activity, suggesting that such a low intake of larvae, even if larvae have a high energy content per unit weight, would not be sufficient for sustaining an aye-aye.

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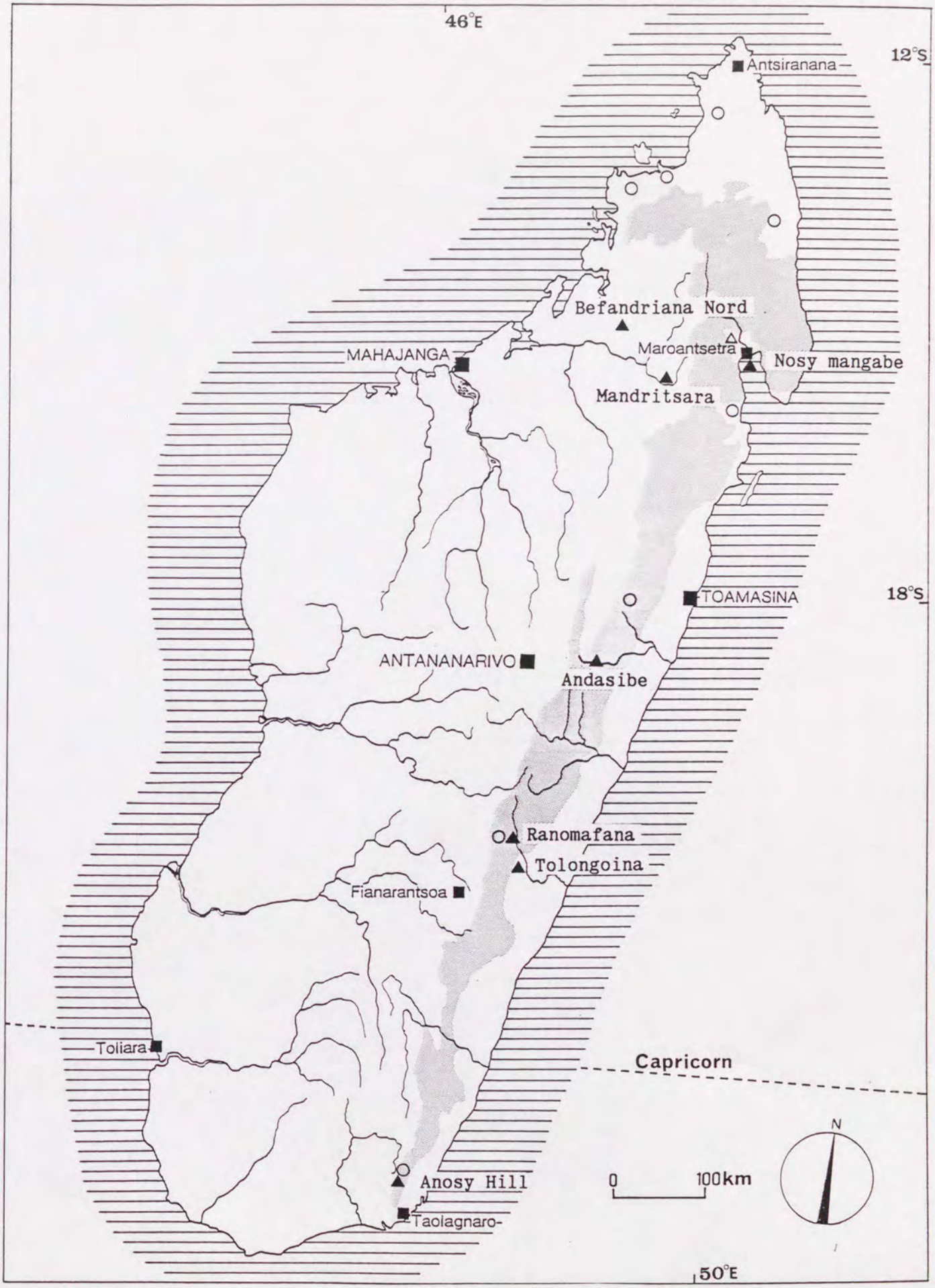

Fig. 1. Distribution of the aye-aye (Daubentonia madagascariensis).

Solid triangle: Existence of the aye-aye (present study).
Circle: Information of the aye-aye (literature).
Solid square: Major city.
Shadow area: Rain forest.

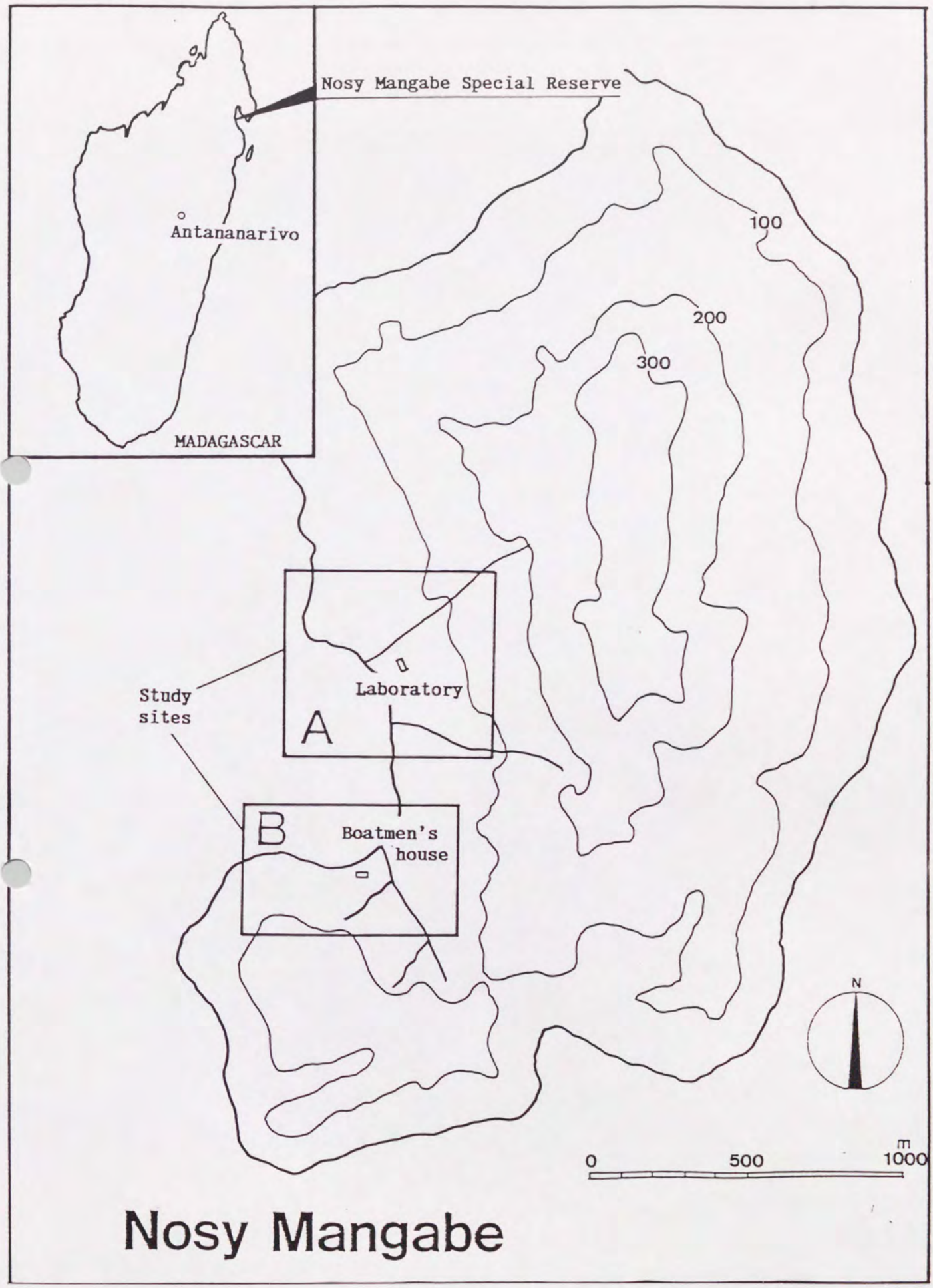

Fig. 2. Area chosen for the ecological study of the aye-aye (Daubentonia madagascariensis).

Fig. 3. The aye-aye feeding on the bark of Afzelia bijuga (July 3, 1989).

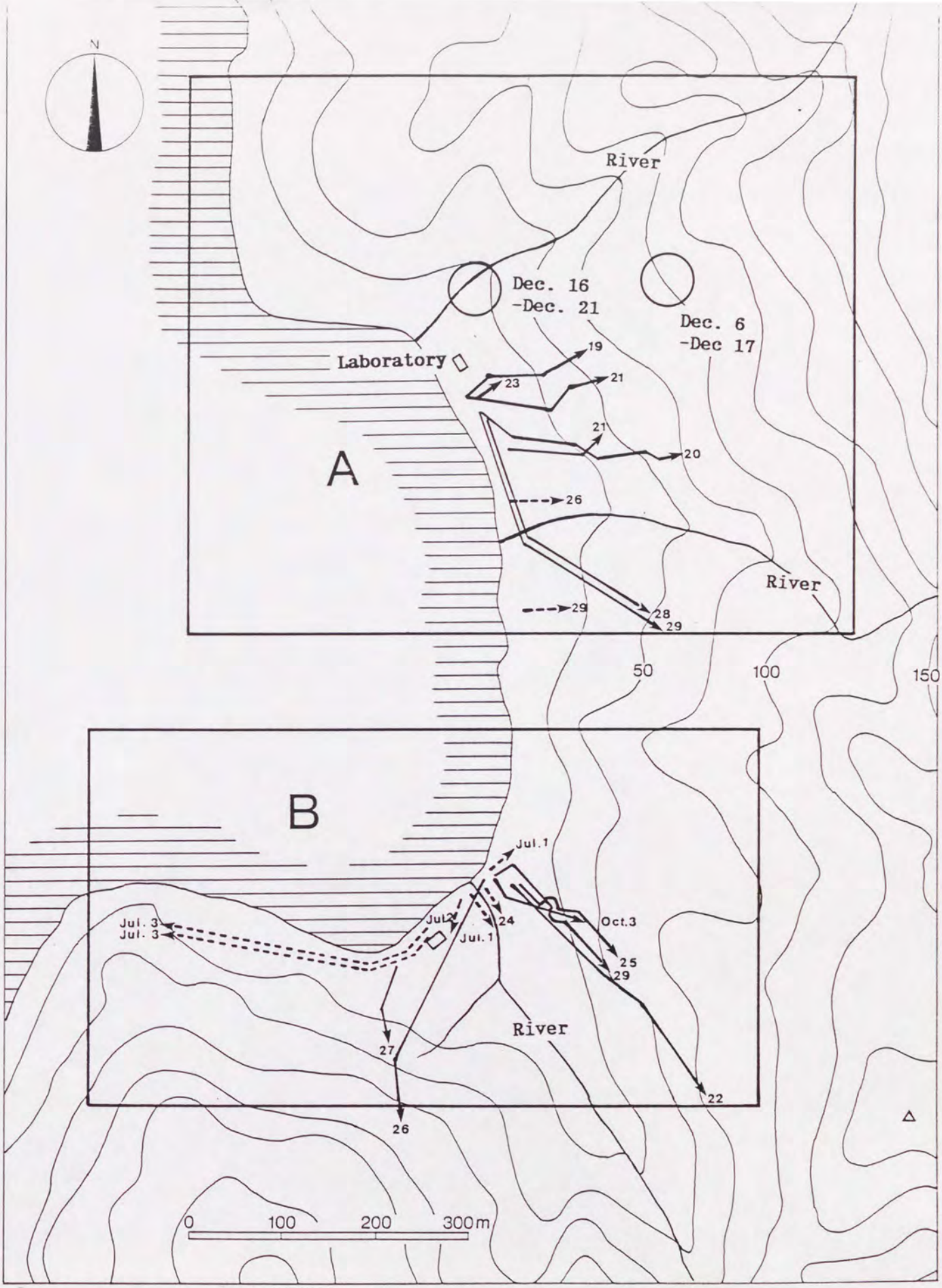

Fig. 4. Tracks of aye-ayes' movement and observation points (December, 1988, June, July, September and October, 1989).

----➤ : June and July, 1989

——➤ : September and October, 1989

○ : December, 1988

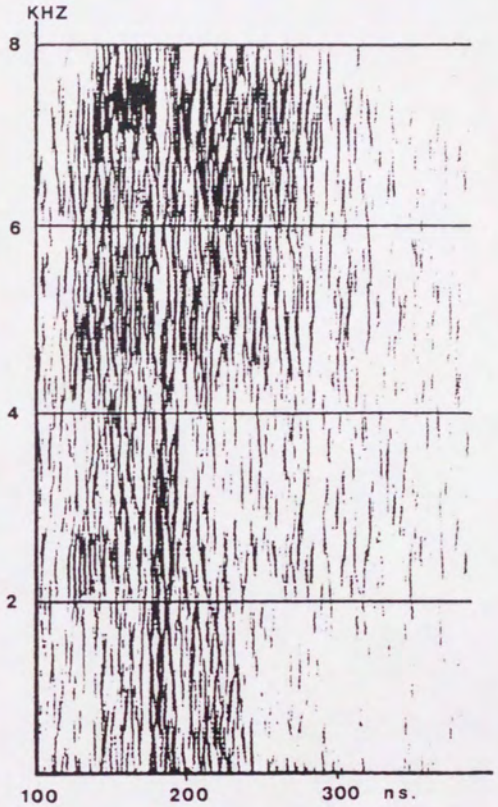

Fig. 5. Sonogram of the aye-aye's call used for communication.

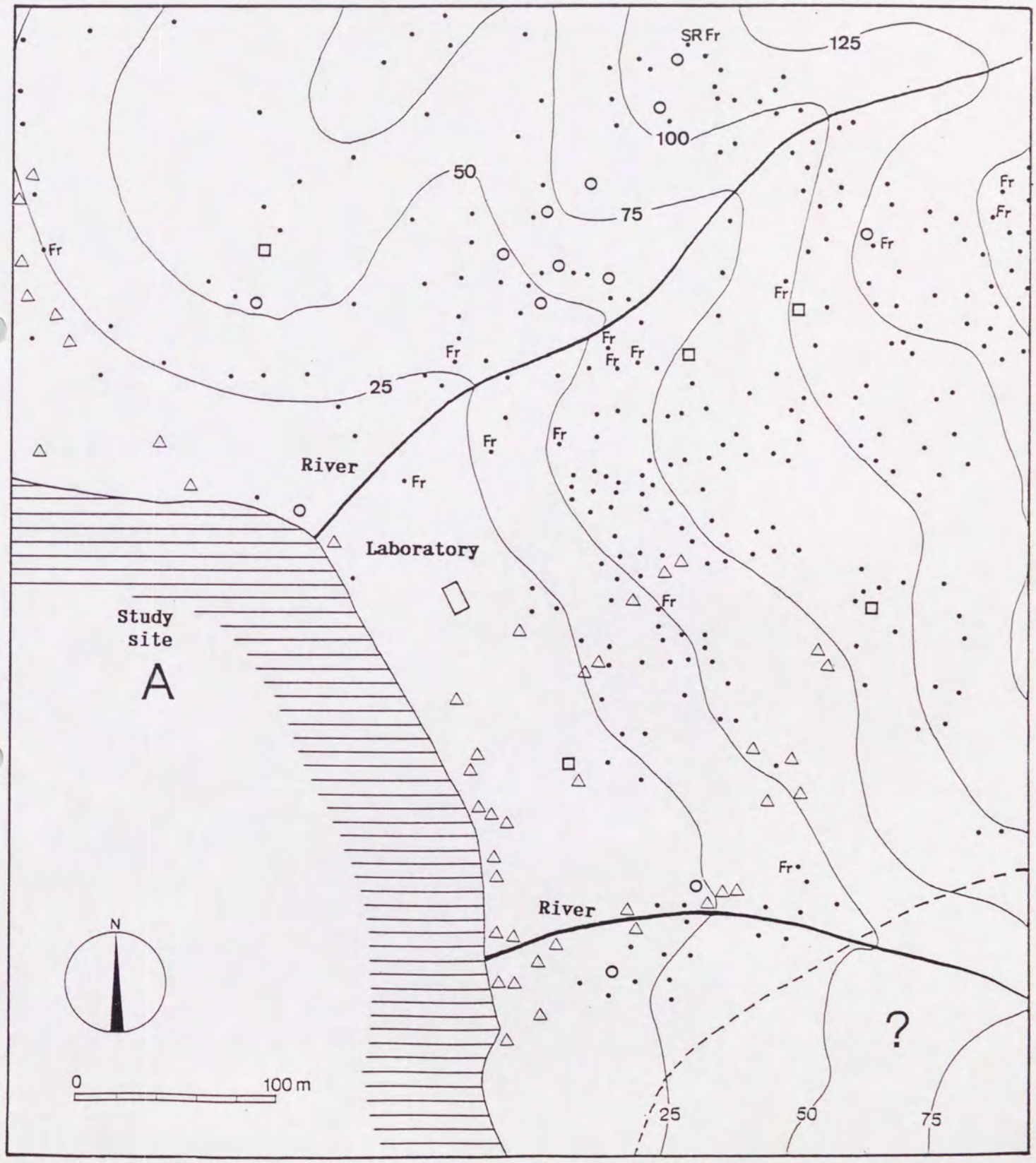

Fig. 6. Distribution of ramy (• for C. Boivini, SR for C. madagascariense), Afzelia bijuga(△), rotten trees (○), and aye-ayes' nests (□) in study areas A.

* Total numbers counted were 281 for ramy, 46 for Afzelia, 13 for rotten trees, and 5 for nests (June 20, 1989).

Table I Temperature and weather at Nosy Mangabe from June to December, 1989

Month	Temperature °C Max.	Min.	Ave.	Weather: Days & %() Fine	Cloudy	Rain	Observation Days
June	21.8	19.7	20.8	2 (14.3)	9 (64.3)	3 (21.4)	14
July	24.4	18.8	22.2	7 (24.1)	16 (55.2)	6 (20.7)	29
August	23.7	18.5	21.3	9 (29.0)	19 (61.3)	3 (9.7)	31
September	24.3	19.4	22.4	7 (25.0)	20 (71.4)	1 (3.6)	28
October	33.0	18.5	24.3	17 (68.0)	7 (28.0)	1 (4.0)	25
November	35.0	19.7	25.3	18 (66.7)	9 (33.3)	0 (0.0)	27
December	34.0	21.2	26.2	15 (50.0)	9 (30.0)	6 (20.0)	30

Table II Food items consumed by aye-ayes and observation samples from December, 1988 to October, 1989

FAMILY Species (Vernacular)	Part eaten	1988 Dec.	1989 Jun. -Jul.	Sept.	Oct.	Total	Percentage
BURSERACEAE							
Canarium Boivini	Nut	354	+	152	109	615	(60.2)
(Ramy)	Bark	3	-	-	-	3	(0.3)
C. madagascariense	Nut	-	+	+	+		
(Ramy/Haramy)							
LEGUMINOSAE							
Afzelia bijuga	Bark	-	142	214	-	356	(34.9)
(Hintsina)							
Entada phaseoloides	Bean	-	-	1	-	1	(0.1)
(Voankarabo)							
EUPHORBIACEAE							
Macaranga cuspidata	Nectar	-	-	32	-	32	(3.1)
(Mongy)							
INSECT LARVAE	Body	-	+	14	+	14	(1.4)
Total		357	142	413	109	1,021	(100.0)

+:Feeding tracks

-:Not observed and no feeding track

Table III Observation samples of feeding by aye-ayes in each hour for ramy and other food items in 1988 and 1989

		Hour											
Food items	Month	18	19	20	21	22	23	0	1	2	3	4	Total
Canarium nut	Dec.	1	2	18	14	136	74	16	42	30	20	1	354
	Sep.	0	0	0	41	0	54	57	0	0	0	0	152
	Oct.	0	0	0	0	25	41	43	0	0	0	0	109
Canarium bark	Dec.	0	0	1	2	0	0	0	0	0	0	0	3
Afzelia bark	Jun.-Jul.	0	0	13	78	51	0	0	0	0	0	0	142
	Sep.	28	91	47	4	12	25	1	0	6	0	0	214
Entada bean	Sep.	0	0	0	0	0	0	0	0	1	0	0	1
Macaranga nectar	Sep.	0	0	8	2	22	0	0	0	0	0	0	32
Insect larvae	Sep.	0	0	13	1	0	0	0	0	0	0	0	14
Total		29	93	100	142	246	194	117	42	37	20	1	1,021

Table IV Seasonal changes in aye-ayes' activity classified by behavior from December, 1988 to October, 1989

Upper: Observation samples, Lower: Percentages

Month	Feeding	Moving	Resting	Social behavior	Vocal communication	Unknown	Total
December	355	355	28	0	18	0	756
	(47.0)	(47.0)	(3.7)	(0.0)	(2.4)	(0.0)	(100.0)
June - July	142	261	47	0	2	5	457
	(31.1)	(57.1)	(10.3)	(0.0)	(0.4)	(1.1)	(100.0)
September	417	753	256	9	5	6	1446
	(28.8)	(52.1)	(17.7)	(0.6)	(0.3)	(0.4)	(100.0)
October	109	113	22	3	4	0	251
	(43.4)	(45.0)	(8.8)	(1.2)	(1.6)	(0.0)	(100.0)
Total	1023	1482	353	12	29	11	2910
	(35.2)	(50.9)	(12.1)	(0.4)	(1.0)	(0.4)	(100.0)

Table V Social contacts of aye-ayes observed in 1988 and 1989

	Hour									
	18	19	20	21	22	23	0	1	2	Total
Contacts of 2 individuals										
Dec. 1988										
Duration	0	1	1	5	2	48	6	31	3	97
No. of occasion	0	1	1	4	2	5	2	3	1	19
Jun.-Jul. 1989										
Duration	0	0	0	0	4	0	0	0	0	4
No. of occasion	0	0	0	0	1	0	0	0	0	1
Sep.-Oct. 1989										
Duration	4	44	37	21	0	0	0	33	0	139
No. of occasion	4	3	4	1	0	0	0	1	0	13
Contacts of 3-4 individuals										
Dec. 1988										
Duration	0	6	0	0	43	5	11	20	0	85
No. of occasion	0	1	0	0	1	1	1	1	0	5
Sep.-Oct. 1989										
Duration	0	0	10	0	0	0	7	35	0	52
No. of occasion	0	0	1	0	0	0	1	1	0	3

Table VI Number of fruiting ramy trees (Canarium Boivini) among 46 samples from June, 1989 to June, 1990

	1989							1990					
	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.
Fruiting													
Many	6	6	6	5	2	0	0	11	11	11	11	11	9
Few	9	4	3	4	2	2	1	1	4	4	2	2	3
Total	15	10	9	9	7	4	1	1	15	15	13	13	12
Percent.	32.6	21.7	19.6	19.6	15.2	8.7	2.2	2.2	32.6	32.6	28.3	28.3	26.1

Fruiting many: More than 10 fruits observed.

Fruiting few: Less than 9 fruits observed.

Percentage: To total (46) samples.

Table VII Nutritional composition and calorie contents of the ramy nut (per 100g edible portion)

Component	Percentage	Method for analysis
Water	7.3	Dry up by heating under normal pressure
Protein	13.3	Kjeldahl method
Lipid	54.2	Soxhlet's extraction method
Ash	4.4	Direct method
Carbohydrate	20.8	100-(Water+Protein+Lipid+Ash)
Energy	584 Kcal/100g	

Appendix I Test of the difference between two proportions of months for three activities

Feeding

	June/July	September	October
December	5.451 p<0.01	8.461 p<0.01	0.973 p>0.05
June/July	-	0.914 p>0.05	3.287 P<0.01
September	-	-	4.613 p<0.01

Moving

	June/July	September	October
December	4.611 p<0.01	9.307 p<0.01	3.198 p<0.01
June/July	-	3.779 p<0.01	0.652 p>0.05
September	-	-	3.53 p<0.01

Resting

	June/July	September	October
December	3.428 p<0.01	2.280 p<0.05	0.533 p>0.05
June/July	-	1.881 p>0.05	3.083 p<0.01
September	-	-	2.064 p<0.05

Appendix II Phenology of the ramy at Nosy Mangabe, 1989

Month		June	July		August		September		October		November		December	
Date		15	15	25	15	25	15	25	15	25	15	25	15	25
C.B.	1	f	F	F	F	F	F	F	F	F	F	F	B	Fl
	2	No	No	No	No	No	No	No	No	No	No	No	Fl	Fl
	3	No	No	No	No	No	No	No	No	No	No	No	Fl	Fl
	4	No	No	No	No	No	No	No	No	No	No	No	No	Fl
	5	O	O	O	O	O	O	O	O	O	No	No	Fl	Fl
	6	No	No	No	No	No	No	No	No	No	No	No	No	No
	7	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	8	No	No	No	No	No	No	No	No	No	No	No	No	No
	9	No	No	No	No	No	No	No	No	No	No	No	Fl	Fl
	10	No	No	No	No	No	No	No	No	O	O	B	Fl	Fl
	11	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	12	No	No	No	No	No	No	No	No	No	No	O	No	Fl
	13	No	No	No	No	No	No	No	No	No	No	No	No	No
	14	No	No	No	No	No	No	No	No	No	No	No	No	No
	15	No	No	No	No	No	No	No	No	O	O	No	Fl	Fl
	16	No	No	No	No	No	No	No	No	O	O	No	Fl	Fl
	17	F	F	F	F	F	F	F	F	F	F	F	Fl	Fl
	18	No	No	No	No	No	No	No	No	No	No	No	No	No
	19	F	F	F	F	f	f	f	No	No	No	No	No	No
	20	F	No	No	No	No	No	No	No	No	No	No	No	No
	21	No	No	No	No	No	No	No	No	No	No	No	No	No
	22	No	No	No	No	No	No	No	No	O	No	No	No	No
	23	No	No	No	No	No	No	No	No	O	No	B	Fl	Fl
	24	No	No	No	No	No	No	No	No	O	No	Fl	Fl	Fl
	25	No	No	No	No	No	No	No	No	O	No	No	B	Fl
	26	No	No	No	No	No	No	No	No	O	No	No	No	No
	27	No	No	No	No	No	No	No	No	O	No	B	Fl	Fl
	28	F	F	F	F	F	F	F	F	F	No	B	Fl	Fl
	29	No	No	No	No	No	No	No	No	No	No	No	No	No
	30	F	F	F	F	F	F	F	F	f	f	No	No	No
	31	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	32	f	f	f	f	f	f	f	f	f	No	No	B	Fl
	33	No	No	No	No	No	No	No	No	No	No	B	B	Fl
	34	No	No	No	No	No	No	No	No	NO	No	No	No	No
	35	No	No	No	No	No	No	No	No	No	No	No	No	No
	36	f	f	f	No	No	No	No	No	No	No	B	Fl	Fl
	37	No	No	No	No	No	No	No	No	No	No	B	Fl	Fl
	38	f	f	f	f	f	f	f	f	f	No	No	No	No
	39	No	No	No	No	No	No	No	No	No	No	No	No	No
	40	No	No	No	No	No	No	No	No	No	No	No	No	No
	41	F	F	F	F	F	F	F	F	F	f	f	f	f
	42	f	No	No	No	No	No	No	No	O	No	No	B	Fl
	43	f	No	No	No	No	No	No	No	O	No	No	B	Fl
	44	f	No	No	No	No	No	No	No	O	No	No	No	No
	45	f	No	No	No	No	No	No	O	O	No	No	No	No
	46	f	f	f	f	f	f	f	No	No	No	No	No	No
C.m.	1	F	f	f	f	f	f	No	No	No	No	No	No	No

Appendix II (continued) Phenology of the ramy in Nosy Mangabe 1990

Month		January		February		March		April		May		June	
Date		15	25	15	25	15	25	15	25	15	25	15	25
C.B.	1	Fl	F	F	F	F	F	F	F	F	F	F	F
	2	Fl	No	No	No	No	No	No	No	No	No	No	No
	3	Fl	No	No	No	No	No	No	No	No	No	No	No
	4	Fl	F	F	F	F	F	F	F	F	F	f	f
	5	Fl	No	No	No	No	No	No	No	No	No	No	No
	6	No	No	No	No	No	No	No	No	No	No	f	f
	7	Fl	No	No	No	No	No	No	No	No	No	No	No
	8	No	No	No	No	No	No	No	No	No	No	No	No
	9	Fl	F	F	F	F	F	F	F	F	F	F	F
	10	Fl	No	No	No	No	No	No	No	No	No	No	No
	11	Fl	F	F	F	F	F	F	F	F	F	F	F
	12	Fl	F	F	F	F	F	F	F	F	F	F	F
	13	No	No	No	No	No	No	No	No	No	No	No	No
	14	No	No	No	No	No	No	No	No	No	No	No	No
	15	Fl	No	No	No	No	No	No	No	No	No	No	No
	16	Fl	No	No	No	No	No	No	No	No	No	No	No
	17	Fl	F	F	F	F	F	F	F	F	F	F	F
	18	No	No	No	No	No	No	No	No	No	No	No	No
	19	No	No	No	No	No	No	No	No	No	No	No	No
	20	No	No	No	No	No	No	No	No	No	No	No	No
	21	No	No	No	No	No	No	No	No	No	No	No	No
	22	No	No	No	No	No	No	No	No	No	No	No	No
	23	Fl	No	No	No	No	No	No	No	No	No	No	No
	24	Fl	No	No	No	No	No	No	No	No	No	No	No
	25	Fl	F	F	F	F	F	F	F	F	F	F	F
	26	Fl	f	f	f	f	f	No	No	No	No	No	No
	27	Fl	No	No	No	No	No	No	No	No	No	No	No
	28	Fl	No	No	No	No	No	No	No	No	No	No	No
	29	Fl	F	F	F	F	F	F	F	F	F	No	No
	30	No	No	No	No	No	No	No	No	No	No	f	f
	31	Fl	No	No	No	No	No	No	No	No	No	No	No
	32	Fl	f	f	f	f	f	f	f	f	f	No	No
	33	Fl	No	No	No	No	No	No	No	No	No	No	No
	34	No	No	No	No	No	No	No	No	No	No	No	No
	35	No	No	No	No	No	No	No	No	No	No	No	No
	36	Fl	No	No	No	No	No	No	No	No	No	No	No
	37	Fl	No	No	No	No	No	No	No	No	No	No	No
	38	No	No	No	No	No	No	No	No	No	No	No	No
	39	No	No	No	No	No	No	No	No	No	No	No	No
	40	No	No	No	No	No	No	No	No	No	No	No	No
	41	Fl	F	F	F	F	F	F	F	F	F	F	F
	42	Fl	F	F	F	F	F	F	F	F	F	F	F
	43	Fl	F	F	F	F	F	F	F	F	F	F	F
	44	Fl	f	f	f	f	f	No	No	No	No	No	No
	45	No	No	No	No	No	No	No	No	No	No	No	No
	46	f	f	f	f	f	f	f	f	f	f	No	No
C.m.	1	F	F	F	F	F	F	F	F	F	F	F	F

Abbreviation of Appendix II

C.B.: Canarium Boivini

No: No fruits
F : Many fruits
f : Little fruits
Fl: Flowering

C.m.: Canarium madagascariense

B: Bud
O: Old leaves

ON USAGE OF THE DIGITS OF A CAPTIVE AYE-AYE (Daubentonia madagascariensis)

IWANO TAIZO

ABSTRACT

A study was carried out between July and August 1989 on usage of the manual digits of one captive female aye-aye (Daubentonia madagascariensis). Manipulation of the digits was examined by direct observation and analysis of images taken with a video-camera.

The third digit, the most slender, and the fourth digit, the longest, are both, whether right or left hand, used for scooping foods and putting them into the mouth: the average duration of one scooping was 11.9 seconds for the third digit and 14.7 seconds for the fourth digit, with no substantial difference between the two digits (t-test, $p>0.05$).

The third digit was also used for percussion. The average duration of one percussion continuum was 2.9 seconds. The fourth digit was often used for grooming, and, when moving, for grasping a twig or holding onto wire mesh.

The aye-aye alternated between usage of the third and fourth digits adaptably according to the foods presented. The third digit was used for scooping out the contents of coconuts, ramy fruits, papayas, passion fruits, bananas, tomatoes, rice, and raw eggs, which were served for experimental purposes. When eating bananas and tomatoes, the fourth digits were mainly used. When eating sugar cane, the third digits were used exclusively for percussion and not for scooping.

KEY WORDS: Aye-aye, Daubentonia madagascariensis, Feeding behavior, Scooping, Tapping, Hard-nut adaptation hypothesis.

INTRODUCTION

The characteristic morphological features of the aye-aye, and especially the singular form of its fingers, have attracted the attention of researchers since its discovery. In particular, the way in which the fingers are used during feeding has been a target of a number of observations (Sonnerat, 1782; Owen, 1863; Petter, 1977; Petter et al., 1977). Those studies, however, were for the most part fragmentary and confined to usage, during feeding, of the third digit, or the most singular in form of all the digits. Nevertheless, percussion using the third digit has not been reconfirmed since the first description by earlier researchers (Petter, 1977). In short, it can be said that no reliable observation has been made on the usage of the fingers of the aye-aye.

In comparison with other primates, the aye-aye has quite specialized morphological traits, including: large continuously growing incisors (right and left incisors which can be moved independently from each other); rodent-like dentition (I:1; C:0; P:0; M:3 for upper, and I:1; C:0; P:1; M:3 for lower); large, movable, membranous ears; claws at the tips of all digits except the great toes; extremely slender third manual digits have a specialized structure, and nipples around the inguinal region (Owen, 1863; Petter, 1977; Tattersall, 1982).

The relationship between the aye-aye's specialized morphological traits and its survival and feeding habits, and the possibility that these characteristic features work cooperatively together to help maintain the aye-aye's existence, especially in terms of feeding activity are questions that first come to the mind when observing an aye-aye, because the aye-aye is far apart removed in its morphology from other primates.

In answer to the above questions, all that I have acquired from previous observations is that the aye-aye extracts the edible parts of hard nuts or the

insides of branches using the third digits and incisors.

The same situation exists regarding studies on the movable, membranous ears of the aye-aye. The only reported observations indicate that they are probably used for searching for insect larvae hidden within branches (Petter, 1977). If our hypothesis that the staple food of the aye-aye is the hard-shelled ramy nut is right (Iwano and Iwakawa, 1988), new insights into the function of the aye-aye's ears would be opened.

A study has been ongoing from June 1989 on the nocturnal activity of the aye-aye fed in the Botanical and Zoological Park of Tsimbazaza, Antananarivo. This study was undertaken to elucidate the nocturnal activity of the aye-aye, including usage of the digits, and the results herein reported were obtained, as a part of this continuous study, between July and August 1989.

METHODS

The adult female aye-aye observed in this study was brought to the Botanical and Zoological Park of Tsimbazaza around September 1988. The animal is reported to have been captured near Antsohihy along the north-west coast of Madagascar, but the details of capture remain unclear.

The aye-aye was housed in a two-part enclosure: a feeding room 2.5m wide, 2.15m long and 2.5m high and a cage 3.8m wide, 3.8m long and 2.5m high. The two parts are separated by a concrete wall with a small window through which the two parts are connected. The side walls and ceiling of the cage, and the rear surface of the feeding room are covered with wire mesh while the front part of the feeding room is fitted with a glass panel. Because the aye-aye ate foods in a dish placed on the floor of the feeding room, I could observe usage of the digits from a very close distance through the glass window.

Period of observations were 13 nights between June 7 and August 30, 1989, and the total direct observation time was 133 hours. The total number of observation units was 15,678 (one observation continuum of 30 seconds duration was taken as one unit), and usage of digits was confirmed to account for about 3% (429 units).

Observations were continued for 11 hours from 18:00 to 5:00 the next day, and recorded following an instantaneous sampling method with a 30 seconds duration (Altmann, 1974). Observations were divided into descriptions of the third and fourth digits, use of the right or left hand, use of digits for feeding and grooming, and the names of foods eaten.

Because the aye-aye was active only in the dark, it was difficult to precisely observe the details of its behavior even in captivity. In addition, the aye-aye used its digits so fast that their movement often escaped observation by the naked eyes. As a means supplementing such defects associated with visual observation a video-camera was introduced for the study of usage of the aye-aye's digits during feeding.

The video-camera was run, apart from the visual observation, over five nights on July 22 and 23, and August 15-17, with the shooting time totaling 209 minutes. When taking videos, two sets of illumination lamps (each of 150,000 lux) were used continuously. Despite the brightness, the aye-aye ate foods facing the light and did not deliberately avoid it.

During this study, the aye-aye was presented with the following foods: coconuts, ramy fruits (Canarium madagascariense), papayas, passion fruits, bananas, tomatoes, sugar cane, rice, raw eggs, honey, coconut milk, and bread (coated with honey or soaked with condensed milk). Studies on feeding were performed using these food items, excepting the last- mentioned three. In addition, an artificial food item was prepared by stuffing sugar cane into the cavity of a bamboo and observations of feeding behavior were recorded.

The aye-aye was given five to seven food items at about 16:00 and thereafter the feeding room was left untouched. When taking videos, however, the feeding method was modified: after the aye-aye was confirmed to be active, a food item was given, and it was exchanged for another only when the animal no longer showed interest in it.

RESULTS

Storage and Preference of Food Items

When the aye-aye was given a whole coconut (July 22), it required considerable time (i.e. 93 min.) before it could eat it. Probably because it became impatient with such long and tedious preparatory work, the aye-aye removed three times pieces of coconut from under the nest box where it had hidden them the day before. Whenever I observed the aye-aye removing a piece of coconut hidden somewhere, I entered the feeding room to search for any other hidden coconut fragments, and removed them if any. Despite such efforts, the animal was frequently observed to take out coconut fragments which were hidden somewhere without my notice.

After taken videos of the aye-aye's feeding on coconuts I exchanged coconuts for eggs. After half an hour, I gave the animal a second egg, which it did not eat, removing instead a piece of coconut hidden at the back of the nest box.

Prior to feeding the next day, the feeder searched for hidden coconut fragments and removed them, if any. The aye-aye, however, again took out pieces of coconuts hidden somewhere. Thus, from then on it was always necessary to search for hidden coconuts before taking videos of the aye-aye's feeding activity. Such food storing habits of the aye-aye have not been reported before.

The aye-aye showed a definite preference toward the test food items. Of the foods given, ramy fruits were consumed most quickly, followed by coconuts and sugar cane. The aye-aye ate bananas, eggs, tomatoes, papayas, rice, passion fruits and bread coated with honey or soaked with milk, but did not eat oranges.

When presented with the artificial food item consisting of a bamboo trunk stuffed with sugar cane, the aye-aye first sniffed it, then tapped it with the third digit, split it by biting, scooped out the sugar cane packed within using the third and fourth digits, and ate it.

Direct Observation on Usage of Digits

Direct observation of the usage of digits was difficult due to the darkness in the feeding room, and the digits were often concealed under the movements of the hands and body. Furthermore, the digits move at speed. Thus, the proportion of movements escaping my attention would be considerable.

(1) Usage of digits classified by types of activities (TABLE I)

A total of 429 observation units were recorded, of which 59% (254 units) comprised usage of the third digits.

Usage of the third digits can be classified into three categories: scooping for feeding, grooming and tapping. The fourth digits were used for scooping and grooming. The fourth digits were also used for grasping branches during moving or hanging on the wire mesh, but such activities were excluded from the present study.

Both the third and fourth digits were used most frequently for feeding (67.7% and 86.8%, respectively). When feeding, the third digit on the left hand and the fourth digit on the right hand were more frequently used. This tendency, however, appeared to be an artifact of sampling and my impression was that the animal positively used both hands with no inclination toward laterality.

Few observation units were recorded during which the third digits were used for grooming, and how they were used was thus also unclear.

Tapping or percussion was done solely by the third digits as far as could be discerned by my observation. This activity was exercised upon various objects such as foods, the surface of trees, the ceiling of the nest box, etc. However, percussion movements were so fast that they often escaped my detection.

(2) Usage of digits classified by food items (TABLE II)

A total of 324 observation units during which usage of digits was confirmed for feeding were recorded. Usage of the third digits accounted for 53% (172), indicating nearly equivalent usage of the fourth digits.

Usage of the third and fourth digits was adaptively discriminated according to the food item eaten: the fourth digits were preferentially used for bananas and tomatoes (about 80%), the third digits were exclusively used for coconuts, ramy fruits and eggs, and for papayas the third digits were used nearly exclusively, except in one case.

Analysis of VTR Records of Usage of Digits during Feeding

A total 109 minutes of video was recorded. Usage of the digits was confirmed to include 334 seconds (117 occasions) for tapping, 1,178 seconds (99 occasions) for scooping with the third digits, and 679 seconds (46 occasions) for scooping with the fourth digits. Judging from the video images the following seven food items were confirmed to be consumed by the aye-aye: coconuts, ramy fruits, bananas, rice, passion fruits, sugar canes and eggs. The aye-aye altered its use of digits depending on the individual food items.

(1) Feeding processes classified by food items

Coconuts (Fig. 1)

In General, coconuts were presented in 5 to 10 cm pieces. The aye-aye

typically held a piece of coconut with both hands, gnawing the pulp with the lower incisors. The two lower incisors of the aye-aye can be used independently from each other, making them effective for scooping out the contents of food items.

When shooting video, I gave the aye-aye a whole mass of coconut, so it had to first open the shell by gnawing. Usage of the digits was different depending on the gnawing process, i.e., the initial process (Process I) from the instant when the aye-aye was given the food until making a large opening in the shell and the successive process (Process II) pursued after the opening is made. Process I consisted of smelling, gnawing and tapping with the third digits (Fig. 1, upper). By contrast, Process II includes the typical feeding activities carried out after a large opening has been made in the coconut shell consisting of eating the contents (embryo and albumen), separately using the third and fourth digits appropriately according to the individual steps. Thus, the fourth digit was used for breaking the contents into large pieces while the third digit was used for effectively carrying the pieces to the mouth.

Ramy nuts (Fig. 2)

In the wild, the aye-aye initially scrapes off the pulp with the incisors and then extracts the embryo within the nut using the third digits. The total feeding time required to consume one ramy nuts was 102 seconds on average (Iwano and Iwakawa, 1988). The aye-aye in captivity, on the other hand, sometimes ate the contents while engaged in widening a hole on the nut surface by gnawing, suggesting that there may be slight differences in feeding behavior between individuals in the wild and in captivity. Aside from such minor differences, however, the basic feeding processes of the aye-aye in captivity did not vary from those observed in the wild as is suggested by the

fact that the feeding time of the aye-aye in captivity on one ramy nut was 103 seconds on average (71-183 seconds, N=4), a value nearly equal to that seen in the wild.

Passion fruits, rice and bananas (Fig. 3)

When given a passion fruit, the aye-aye smelled, tapped, bored a hole into the pulp by gnawing, broke through the hole by inserting the fourth digit, and extracted the contents using the third digit. The aye-aye, however, apparently did not favor passion fruits, because it refused to eat a second fruit after consuming a first one.

At first the aye-aye ate rice with its mouth directly, but later switched to using the third and fourth digits to carry it to the mouth.

Of all the observation units during which feeding on bananas was confirmed, about 80% showed usage of the fourth digit. Analysis of the video images also demonstrated that about 91% of the time consumed for scooping up the content of bananas consisted of usage of the fourth digit.

Sugar cane and eggs (Fig. 4)

The aye-aye did not engage in scooping with the digits for feeding on sugar cane. While eating sugar cane, the aye-aye frequently tapped the cane stem with the third digit in intervals between biting the pulp and sucking the juice, as if searching for a location more vulnerable to a bite.

By biting, the aye-aye bored a small opening into the egg-shell through which it extracted the contents by scooping out with the third digit. When feeding on eggs, the third digit was used continuously for long periods (maximum of 178 seconds).

(2) Continuous use of digits

The average time span during which the third digit was continuously used for tapping remained the same regardless of whether it belonged to the right or left hand (2.9 seconds for the left and 2.8 seconds for the right).

When feeding on ramy nuts, the aye-aye initially eating only after smelling without engaging in tapping or other such preparatory inspections which are commonly performed for other food items. This behavior suggests its familiarity with this particular food item. In this connection, it is noteworthy that the aye-aye, when given an unripe ramy fruit, simply sniffed to refuse it, without showing any sign of tapping.

In general, the average time span consumed during feeding for scooping by the third digits (11.9 seconds) showed no substantial difference from that for the fourth digits (14.7 seconds; t-test, $p>0.05$). When feeding on bananas, the third digits (both right and left) were used for scooping for a span of 3 seconds on average while the fourth digits were used for 13.7 seconds on average for the right and 32.8 seconds for the left; i.e., the fourth digits were preferentially used regardless of laterality.

The average time spent scooping was greatest when feeding on eggs (47.1 seconds, N=8), equivalent to five times the average time span (9.2 seconds) for other food items. Another feature to be noted in feeding on eggs is that the aye-aye did not change hands in usage of the digit during scooping.

The average time spans for scooping during feeding on coconuts and ramy fruits were 8.4 seconds (N=52) and 11.8 seconds (N=10), respectively. The two values were virtually no different (t-test, $p>0.05$).

The average time span for scooping by the fourth digits was slightly longer for bananas (21.2 seconds, N=10) than for coconuts (14.4 seconds, N=28; t-test, $p<0.05$).

DISCUSSION

The aye-aye puts its digit into the mouth and scoops up food by using the digit like a tongue. The aye-aye uses both the third and fourth digits for

this purpose, but the third digits seem to be more adapted for this activity because they are very slender, less than half the size of the fourth digit.

This singular feeding behavior of the aye-aye, i.e., eating food with the fingers, has long since attracted much attention, solid observational data is still lacking. Sonnerat (1782, quoted in Owen, 1863) reported, "the animal makes use of the middle digit to draw out of holes in trees the worms which form its food." Thus, this early investigator contended that the third digit was used for feeding insect larvae.

Sandwith (in a letter quoted in Owen, 1863) reported that the aye-aye tapped with the third digit on the bark of a branch possibly hiding insect larvae, inserted the digit into a hole, bit away the bark, and took out the larvae to eat. He added further that the third digit was also used for drinking water.

Substantial additions to those early observations, which were done immediately after the discovery of the aye-aye, have been made by later researchers, who clearly noted that the aye-aye fed in the wild on insect larvae, coconuts, litchis, mangoes and the sap of Hintsyna (Afzelia bijuga), and further, under human care, the aye-aye ate bananas, raw eggs, rice boiled in soup, sugar cane and honey. These observers further demonstrated that the aye-aye used exclusively the third digits for eating coconuts, insect larvae and eggs, and combined use of the fourth digits for eating bananas (Petter and Peyrieras, 1970; Petter, 1977; Petter et al., 1977). They did not, however, confirm usage of the third digit for percussion ("We have never observed, however, the third finger used as a percussion instrument, as has been described by early observers." :Petter, 1977).

Recently, aye-ayes have been directly observed in the Nosy Mangabe Special Reserve, and based on such observations, the bark of Hintsyna (Afzelia bijuga), bamboos (Bambusa vulgaris, Pollock et al., 1985), and nuts of ramy

(Canarium madagascariense, Iwano and Iwakawa, 1988) were newly added to the diet of the aye-aye in the wild. Although the third digit was found to be used for eating ramy nuts, it was never observed to be used for percussion.

Examination of the skeleton (Parc Tsimbazaza, No. 1262) of a young adult male aye-aye stored in the specimens room of the Botanical and Zoological Park of Tsimbazaza (Table III) showed that the metacarpal is continuous with the third digit and protrudes about 18mm from the palm. Furthermore, the joint with the phalanx is so firmly fixed that the third digit cannot grasp a branch nor be used to hang as can the fourth digit. Namely, the third digits appear to be specially adapted for scooping during feeding, grooming and percussion. When using the third digit for percussion the aye-aye slants its large, membranous ears forward, apparently to listen to the sound generated by percussion (Fig. 5), suggesting a close relationship between these two specialized structures (the digit and ears).

I assume that the aye-aye's ears play a role detecting the thickness of the shell of a nut or the nature of its contents (insect larvae also are one of the contents) by analyzing the sound reflected from the object when it is tapped with the third digit. Thus, I find it unlikely that ears are for perceiving the sounds generated by insect larvae crawling within a branch.

In this connection, it should be added that when the aye-aye gnaws on a hard object, tension upon its face is increased, which sometimes results forward and downward movement of the ears.

During feeding, the joint of the third digit can either be bent ventrally or dorsally (Fig. 6). During this sequence, the third digit was moved as flexibly and smoothly as if it had no bone in its interior. The third digit appears to be markedly different in structure from other digits, but this question cannot be solved without more detailed study on its structure and

function.

The aye-aye alternates its usage of the third and fourth digits according to food items, which may be principally related with the structure of the fourth digit. The fleshy part beneath the claw of the fourth digit does not widen as do other digits, excluding the third digit (compare the second and fourth digits holding the tomato in Fig. 7). This fact suggests that the fourth digit is always used in association with feeding.

The claw of the fourth digit is more than two times longer and wider than that of the third digit, and as a whole the fourth digit is stouter than the third digit. When feeding on passion fruits, the aye-aye, after peeling off the pulp with the incisors, at first used the fourth digit. This can be explained by assuming either that the hard shell can not be broken open by the third digit or that operations requiring more skill and force are allotted to the fourth digit. This assumption was apparently corroborated by observations of feeding on coconuts. The aye-aye, immediately after making a large opening in the shell with its incisors, extracted the contents while simultaneously breaking it into pieces with the fourth digit, thereby making it easier to use the third digit for feeding thereafter. The fourth digit was mainly used for eating bananas and tomatoes. This is probably because the fourth digit can scrape out a greater quantity in one stroke than the third digit can.

Why does the aye-aye use the digits to feed on such food items as bananas, tomatoes, papayas, and uncooked rice and eggs, which would be more efficiently consumed through the mouth directly? This may be explained by the feeding behavior of the aye-aye in the wild. It has been demonstrated (Iwano, in press) that ramy nuts (Canarium spp.) constitute the staple food of the aye-aye, as postulated by Iwano and Iwakawa (1988). Feeding on those fruits would be impossible without using the third digit, or some type of gouge. This also holds true for feeding on another important food item of the aye-

aye, the wood-boring insect larvae. Because they preferentially inhabit dead trees, scooping the larvae out with a slender digit represents a quite effective feeding method. It is possible that the aye-aye is so deeply adapted to such feeding methods that it also applies the same methods to novel food items.

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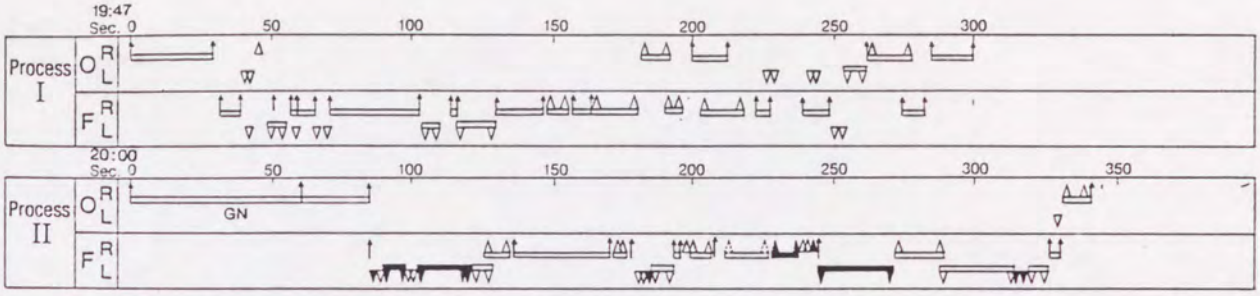

Fig. 1 Feeding process of the aye-aye on coconut (July 22, 1989).

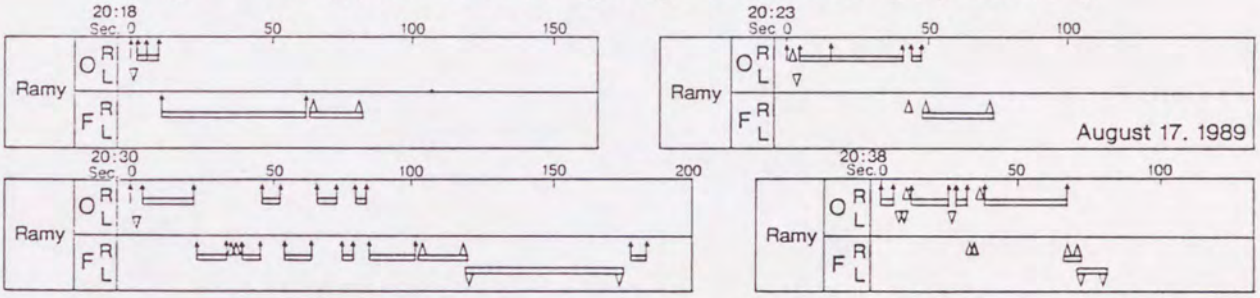

Fig. 2 Feeding process of the aye-aye on ramy nuts (August 17, 1989).

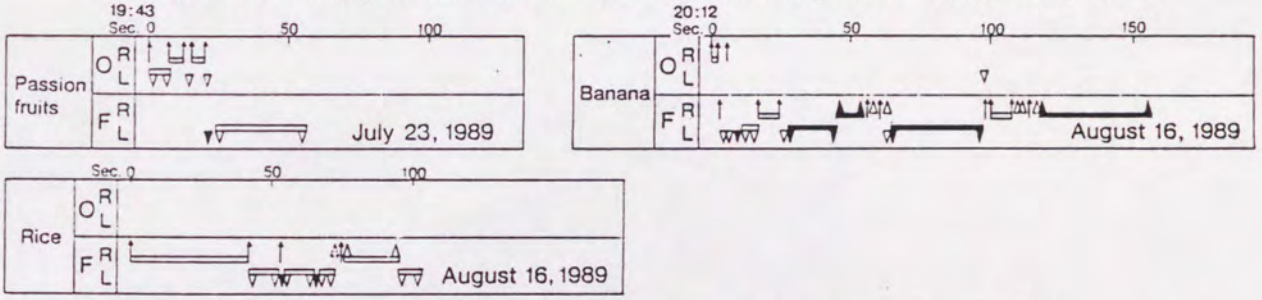

Fig. 3 Feeding process of the aye-aye on various foods (1).

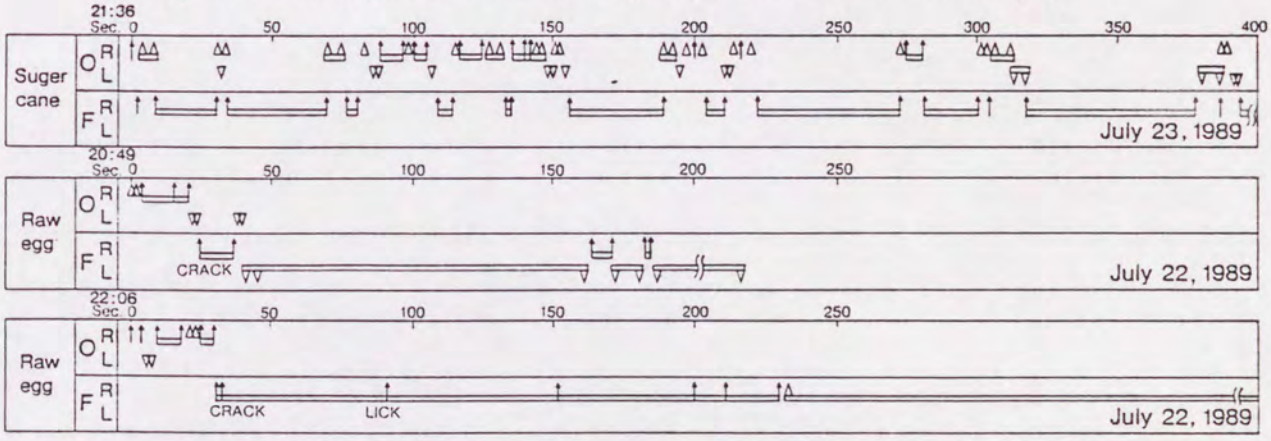

Fig. 4 Feeding process of the aye-aye on various foods (2).

O:Tapping etc. R:Right hand △ 3rd digit ▲4th digit △ 3rd or 4th digit unidentified = Right hand
F :Feeding L:Left hand ▽ 3rd digit ▼4th digit ↑ Gnaw, smell and licking — Left hand

Fig. 5 The aye-aye used the third digits for tapping on the surface of sugar cane.

Fig. 6 The aye-aye sometime used the third digits to feed tomatoes.

Fig. 7 The aye-aye ordinarily used the fourth digits to feed tomatoes (81.6%).

Table I Comparison of usage 3rd and 4th digits for various activities measured by the instantaneous sampling method between July 9 and August 30, 1989

(One unit is 30 seconds duration)

	Third digit						Fourth digit						
	Right	%	Left	%	Total	%	Right	%	Left	%	Total	%	Total
Feeding	53	(51.5)	119	(78.8)	172	(67.7)	93	(90.3)	59	(81.9)	152	(86.3)	324
Grooming	18	(17.5)	10	(6.6)	28	(11.0)	10	(9.7)	13	(18.0)	23	(13.1)	51
Tapping	32	(31.1)	22	(14.6)	54	(21.3)	-	-	-	-	-	-	54
Total	103		151		254		103		72		175		429

Table II Comparison of usage of 3rd and 4th digits for feeding on various food items measured by the instantaneous sampling method between July 9 and August 30, 1989

(One unit is 30 seconds in duration. Lower values are percentages of total units.)

	Banana	Tomato	Papaya	Coconut	Ramy	Egg	Bread	Others	Total
Digit									
3rd Right	11	1	4	12	17	7	1	0	53
	(36.7)	-	-	-	(34.0)	(17.5)	-	-	(30.8)
Left	19	6	11	10	33	33	1	6	119
	(63.3)	-	-	-	(66.0)	(82.5)	-	-	(69.2)
Total	30	7	15	22	50	40	1	6	172
4th Right	71	21	1	0	0	0	0	0	93
	(59.2)	(67.7)	-	-	-	-	-	-	(61.2)
Left	49	10	0	0	0	0	0	0	59
	(40.8)	(32.3)	-	-	-	-	-	-	(38.8)
Total	120	31	1	0	0	0	0	0	152

Table III Size of the aye-aye's manual digits

(Sample No. 1262, Parc Tsimbazaza)

L :Length, W :Width (unit:mm)

	Claw		Second		Third		Metacarpus		Total length
	L	W	L	W	L	W	L	W	
Right hand									
Pollex	16.9	3.9	21.2	6.8	-	-	-	-	38.1
Index	16.5	2.6	20.2	3.9	31.0	3.9	-	-	67.7
Medius	7.6	1.4	17.6	1.9	41.9	2.7	17.7	4.3	84.8
Annularis	16.7	3.2	37.2	4.3	49.1	5.1	-	-	103.0
Minimus	15.9	3.8	24.0	4.4	33.5	4.2	-	-	73.4
Left hand									
Pollex	18.3	-	20.9	5.9	-	-	-	-	39.2
Index	17.0	2.7	20.3	3.7	31.2	4.2	-	-	68.5
Medius	7.8	1.3	18.8	1.9	42.7	2.6	17.8	3.7	87.1
Annularis	16.5	3.2	37.3	4.7	52.4	5.2	-	-	106.2
Minimus	16.8	3.0	24.3	4.2	34.8	4.3	-	-	75.9

NOCTURNAL ACTIVITY OF A CAPTIVE AYE-AYE (Daubentonia madagascariensis)

IWANO TAIZO

ABSTRACT

The activity of one captive female aye-aye was observed for a total of 371 hours over 35 nights between June and November 1989.

The aye-aye was nocturnal and active at any time at night, but from 2:00 hrs in the morning till just prior to dawn it often took a rest. In addition, it frequently returned to the nest to take a long rest (more than half an hour).

The aye-aye's activities were classified into four categories; i.e., feeding, moving, resting and other activities. The average proportions of these activities were 14.8%, 25.3%, 56.7% and 3.2%, respectively. Such proportion of the activities showed seasonal changes. Rises in atmospheric temperature were highly correlated with increases in the proportion of moving ($r=0.908$). Generally speaking, feeding was high in the early and gradually fell toward the later at night.

Four activities were sub-divided into several component acts such as eating, drinking, walking, hanging, sitting, sleeping, tapping, gnawing, etc. In terms of component acts constituting those activities, hanging was positively correlated with a rise in temperature ($r=0.889$), while sitting was negatively correlated ($r=-0.862$), suggesting that the activity of the aye-aye is generally enhanced with rises in atmospheric temperature.

The aye-aye was observed to engage in tapping and gnawing on any night during the period. These acts consisted of a long series of gnawing at definite places on the window or the iron frame of the door.

During the period of study the aye-aye was fed with 12 items of diet such as coconuts, ramy nuts, bread, bananas, honey, eggs, tomatoes, sugar cane, papayas, palm fruits, pineapples and milk. The weight of food consumed during meals was measured over 16 nights to calculate the energy intake of the aye-aye, which was found to average 306.1 kcal per meal.

The response of the aye-aye to light was markedly different from other nocturnal prosimians. The aye-aye was not apparently disturbed when exposed to intense lights.

Key Words: Daubentonia madagascariensis, Aye-aye, Nocturnal activity, Food, Feeding behavior, Energy intake, Hard-nut adaptation hypothesis.

INTRODUCTION

Since its first discovery in the 18th century, a small number of aye-ayes have been kept privately as well as in public facilities such as zoos (Bartlett, 1862; Owen, 1863; Millot, 1952; Petter et al., 1977). However, no quantitative, long-term surveys on the nocturnal activity of aye-ayes in captivity or in the wild, have ever been conducted. Recently, Winn (1989) started a study at the Paris Zoological Garden on three individuals which had been captured on the east coast of Madagascar in 1986 (Albignac, 1986), and reported a number of important observations, especially regarding mother-infant relationships. Despite such recent trends, until now, no quantitative study has been presented on the nocturnal activity of aye-ayes.

Through observation of wild aye-ayes at Nosy Mangabe, I gained some insights into the hourly changes of aye-ayes' daily activities, such as feeding (Iwano, in press, a). However, the result was far from complete in disclosing the nocturnal activity of aye-ayes, owing to my inability to follow

aye-ayes' activities at dark for a considerable portion of the observation time. Our experience indicates that difficulties in the direct observation of aye-ayes' behavior are due to the following factors: the aye-aye's activity is nearly completely nocturnal, that is, its activity is observable only at dark; it usually moves through the crown of tropical rain forests; it moves singly apart from other conspecifics; it rarely vocalizes; and it often hides in thickets when resting.

This investigation was carried out at, and under the auspice of, the Botanical and Zoological Park of Tsimbazaza (Tsimbazaza Zoo), Madagascar Democratic Republic. The aim of the study was to elucidate the nocturnal activity of one adult female aye-aye housed at the park.

The activity of a captive aye-aye will, of course, be more or less different from that in the wild, but the study of its nocturnal activity should contribute in gaining an insight into the ecological picture of the aye-aye at large.

I also focused on the feeding habits of the aye-aye in an effort to explain preferences toward certain diets in terms of their energy content, and to determine the degree to which the preference of the aye-aye toward certain foods is related to its specialized morphological traits.

STUDY SITE AND METHODS

Study Site

Antananarivo, the capital of Madagascar (1381m above sea level and 18° 56'S), is situated in the highland area of the central part of Madagascar. Its temperature averages 17.3 °C annually. In terms of monthly average temperature, July is the lowest (13.3°C) and January is the highest (20.1°C). The difference between the highest and lowest temperatures within a day ranges from 6 °C to 16 °C (Donque and Petit, 1967; Donque, 1972).

The annual precipitation at Antananarivo is 1354mm or half that of the forested regions along the east coast, such as Maroantsetra. The average monthly precipitation is highest in January (309mm) and lowest in July (7mm) (Donque and Petit, 1967).

Methods

The aye-aye under study, an adult female, was one that had been fed since 1988 at the Tsimbazaza Zoo, Antananarivo. It is reported that this animal had been captured by some local inhabitant near Antsohihy on the west coast of Madagascar and was then protected by a press agent who later donated it to the zoo.

The animal was housed in a two-compartment feeding facility consisting of a cage (14.6m^2), whose ceiling and sides were covered with iron mesh, and a feeding room, (5.4m^2) which was equipped with a nest box and fitted with a front glass panel (Fig. 1). Food was placed on the floor of the feeding room, and the aye-aye, coming out of the nest box at night, consumed the food which was placed on the floor. Food was given once-a-day from 4 to 5 o'clock in the evening, and the quantity was sufficient to meet the appetite of the aye-aye, as was evidenced by the fact that the aye-aye always left behind an unconsumed portion. Unconsumed food was removed the following morning.

The study period lasted for 35 nights between June and November 1989. The total observation time was 371 hours, or 43,375 30-sec samples based on the instantaneous observation method (or 43,369 in terms of instances of observation) (Table I). In addition, as part of another series of studies I measured the consumed weight of individual meals for 16 nights between September and November, to calculate their respective energy values.

1. Observation of the Aye-aye's Activities Based on the Instantaneous Method.

Observation of the aye-aye's activities was carried out over half a year during a seasonal change from winter to summer. Although this cannot provide sufficient data to obtain a full understanding of annual changes in the aye-aye's activities, it allows me to gain an insight into their seasonal change of habits. The results regarding manipulation of the aye-aye's digits are to be presented elsewhere (Iwano, in press, b).

Observations were carried out from 6:00 hrs in the evening until 4:59 hrs the next morning. Observations prior to and following that interval were excluded from the study, because the aye-aye was virtually inactive.

The aye-aye was observed to be active at 4:00 hrs in the evening in May (Mr. Rakotoarisoa; the curator of Tsimbazaza Zoo, personal communication), and there was information suggesting that along the west coast of Madagascar aye-ayes are occasionally active during daylight hours (probably evening) in October (Mr. H. Fukazawa, personal communication). Thus, it is likely that aye-ayes occasionally become active when it is still light. Even allowing for such divergent activity, however, I think the observation period totaling 11 hours between 18:00 and 5:00 covers a major part of the aye-aye's activity.

In accordance with the instantaneous sampling method (Altmann, 1974), I considered the aye-aye's activities in terms of units, each of 30 sec duration, and recorded the location of the aye-aye and the type of activity for each unit. Such observation units will be referred to as samples hereinafter.

Although this method does not always allow one to sample brief activities ending within 30 sec such as jumping, tapping, etc., principal activities determining the aye-aye's activity pattern such as sleeping, feeding, etc., owing to their comparatively long duration, could be fully covered with this method.

The aye-aye's activities were defined in terms of place and type.

(1)Gross categories of place of activity (place)

The place where a given activity of the aye-aye occurred was roughly classified into two areas; the cage and the feeding room. The activity site was further divided into minor categories. For the cage, sub-categories included "on the ground", "on tree branches", and "on wire mesh" (the sides and ceiling of the cage were fitted with mesh on which the aye-aye often climbed or clung). For the feeding room, on the other hand, the place of activity was subdivided into the following minor categories: "on the ground", "on tree branches", "on wire mesh" (the feeding room also had wire mesh on the wall facing the aisle), "in the nest box", "on the roof of the nest box", "under the nest box", "behind the leaves" (a tree branch covered in leaves dense enough to hide the aye-aye's body was placed in front of the nest box), and "on the window" (which was installed as a passage on the wall dividing the feeding room and cage).

(2)Gross categories of activities (activity)

The aye-aye's activities were roughly divided into four categories: feeding, resting, moving and other activities. Minor categories of the activities (act): These four general activity categories were further subdivided into elementary acts as follows.

Feeding was subdivided into eating and drinking. When the aye-aye was given a coconut, it ate the edible meat and drank the milk within it simultaneously. The two acts were so inseparably mixed that they were classified under the same feeding category.

Moving was subdivided into walking, climbing, hanging and jumping.

Resting was subdivided into standing, sitting, sleeping, self-grooming, and suspending. Suspending differs from common hanging in that the suspending animal is motionless for a span of at least 30 seconds, whereas common hanging

indicates that the animal is on the move. Sleeping can be distinguished from sitting in form. For example, when the animal takes a rest on the ceiling of the nest box, it crouches, coils its tail on its ventral aspect, and directs its head inward, while in sitting it sits with its rump on the floor and remains motionless. Coiling the tail inward under the body is a characteristic posture indicating the animal is in a relaxed state. Entry into and sojourn in the nest box was also interpreted as sleeping, although I could not determine exactly what activity the animal was engaged in.

Other activities include a variety of elementary and complex acts, such as excreting of urine and feces; gnawing at trees, window-frames and the iron parts of the door; tapping something with the finger tips; smelling; licking something other than foods; holding something including foods; pulling tree branches outside the nest box from within the nest box; and playing. Playing is a compound activity including a number of elementary acts, and consists of various brief actions such as running with something in the mouth, tumbling about on the floor, lying on the back on the floor, etc. However, I feel it is more reasonable to consider a series of such acts as one whole rather than to reduce them into individual acts and assign each of them to appropriate act categories. Thus, such actions were classified as a whole under the same category of playing.

To facilitate observation, torch light was shone directly upon the aye-aye, which was apparently not disturbed by such artificial intervention. Moreover, for close observation, I often came within 20 cm of the aye-aye, with the glass panel between us, but the animal remained unresponsive to such intrusion. This characteristic coolness of the aye-aye toward external changes was further demonstrated by its behavior during video recording: Two lights, each of 150 thousand lux, were shone onto the animal from about 2m, but this drastic illumination did not appear to have the slightest effect on

its behavior, and the animal even ate food when facing the light. Thus, light and the presence of humans in close proximity to the animal had practically no effect on it. However, the animal apparently paid attention to signs and sounds of human presence behind the door of the feeding room placed opposite the glass panel, and sometimes even fled beneath the nest box.

2. Measurement of Food Intake

For 16 nights between September and November 1989 I measured food intake. Using a platform scale, I weighed foods given and the unconsumed remains, and food intake was obtained by subtracting the latter from the former. The total energy intake was calculated from the food intake data.

3. Data Analysis

Observation of the aye-aye's nightly activities was analyzed by the hour under the following categories: place of activity, type of activity, kind of acts constituting each activity, and feeding behavior on individual food items. For each categories, the relevant samples were summed and their proportion relative to the gross total (%) was calculated.

The aye-aye's activity varied from night to night: one evening the animal would start to eat as soon as it woke up and exited from the nest box; another night it would take a long rest after coming out of the nest box; and still another night it would move around awhile before sitting down to eat. This variety was reflected in the recordings of the aye-aye's nightly activity, where the proportions of individual activities varied considerably from night to night.

To obtain a general pattern of the aye-aye's nightly activity, the data were analyzed for each month, and the monthly data thus obtained were compared with each other. More detailed analyses involved examination of hourly

changes in individual activities and the average single duration of principal acts constituting an activity. All of these data were inspected to determine seasonal patterns in activities, including their component acts. Nutritional approaches to food intake of the aye-aye were treated as a separate subject.

RESULTS

1. Seasonal Change in Activity Pattern as Analyzed from Its Component Acts

The data of the aye-aye's nightly activity were summed for each month from August to November (Table II). For each month, samples of a given activity were summed, and the total was expressed as a percentage of the gross total. Then, the relative distributions of individual activities were compared between different months. For June and July, however, the data were combined together. Two samples each in July, August and September (six in total) could not be ascribed to any definite activity category, but observation records were continued. Thus, the total numbers of activity samples (43,369) is six units less than the total numbers of observation samples (43,375).

(1) Resting

The monthly relative distribution of resting was dominant among individual activities throughout all the months studied. Resting was followed by moving, feeding, and other activities, in that order. The high proportion of resting can be partly explained by the fact that the aye-aye often entered the nest box to take rests lasting 30 minutes to one hour.

The longest total duration of resting ever observed in my study was 7 hours on August 11 to 12 (which included a continuous stretch of 5 hours from 0:00 to 4:59 hrs), and the proportion of resting on that day was 90.7%, the highest of all the resting proportions. Observation records for October 16 to

17 showed the longest continuous rest 4 hours in length, with brief stretches of resting occurring frequently throughout the observation period, thus resulting in a high resting proportion of 85.1%. The same tendency was observed on August 13 to 14 when the proportion of total resting was 72%, with the longest continuous rest lasting 5 hours from 21:00 to 1:59 hrs. Observation periods in which the total duration of resting exceeded 3 hours occurred on nine nights.

Thus, owing to the aye-aye's predilection to rest for long continuous periods as well as brief and frequent intervals, the relative monthly activities of the aye-aye was found to be predominantly occupied by resting. Resting accounted for more than 50% of monthly activities except in November. The resting proportion was compared among different months, and significant differences were found (test of the difference between two proportions, $p<0.05$), except for following pairings: June/July and November, and September and November.

(2) Seasonal change in activity proportions (Fig. 2)

The relative distribution of individual activities showed seasonal (or monthly) changes. The proportion of "other activities", however, did not show such seasonal changes: It remained virtually invariable from June to October, except in November when the proportion was significantly different from that in other months.

The monthly proportion of feeding showed a falling tendency from 18% in June/July to 11% in November with, however, no significant difference between August and October (test of the difference between two proportions, $p>0.05$).

The most conspicuous seasonal change is existent in the monthly activity proportions of moving. The moving proportion in June/July was nearly equal to the corresponding feeding proportion, whereas in November, it rose to three times the value of the corresponding feeding proportion. The ratios between

the moving and feeding proportions were significantly different for all months compared (test of the difference between two proportions, $p<0.05$), except those between September and October.

The proportion of "other activities" in November was significantly higher than that in any other month (test of the difference between two proportions, $p<0.01$). This difference was due to the fact that tapping and gnawing, two principal components of "other activities", increased in November.

(3) Seasonal change in individual acts

The principal acts constituting moving are walking and hanging. Hanging rose from 3.3% in June/July to 14.5% in November. In contrast, walking did not show any noticeable change through the months studied, except in November (test of the difference between two proportions, $p>0.05$).

The seasonal changes observed in activity were reflected in changes in the use of place. Use of wire mesh increased from 5.2% in June/July to 20.6% in November. The use of tree branches also increased from 2.9% in June/July to 17.6% in November. In summary, the aye-aye was active outdoors in November and especially preferred to move along tree branches or hang from wire mesh.

Elementary acts constituting resting included sitting, self-grooming and sleeping, and their monthly proportions were found to differ significantly from month to month showing seasonal changes (test of the difference between two proportions, $p<0.05$).

Among the elementary acts involved in "other activities", tapping and gnawing showed a characteristic seasonal change, that is, their monthly proportion was high only in November. On the other hand, excreting remained constant throughout all months studied.

In November, the aye-aye tended to display unusual behaviors and diversified activities, as well as an increased frequency of gnawing and

tapping, as previously noted. Unusual activities included a series of playful actions, such as rolling about on the floor, jumping, holding something in the mouth, or a combinations of those actions.

"Pulling", or pulling twigs into the nest box, was initially observed in October, and its proportion increased in November. This act may be related to nest building for breeding, but nest-building did not actually result.

(4) Relation of activities and component acts with temperature

The aye-aye's proportion of feeding showed a gradual decrease from June/July to November (although the decrease was leveled off between August and October), while the proportion of moving gradually rose (although the lowest level was reached in August). A comparable tendency was observed in the monthly change of atmospheric temperature in the region. When the monthly change of individual activities was compared with that of the average monthly temperature at Antananarivo (see Table II), that only the moving proportion was found to show a significant positive correlation ($r=0.908$, $p<0.05$).

Among the component acts constituting moving activity, the hanging proportion showed a positive correlation ($r=0.889$, $p<0.05$), while among resting activities, the sitting proportion was negatively correlated with temperature ($r=-0.862$, $p<0.05$).

The walking proportion remained unrelated to temperature ($r=0.608$, $p>0.05$).

Obviously, not of all aye-aye's activities can be explained simply by temperature changes in its environment. However, because the study period corresponded with a transition from winter to summer, when a most drastic change takes place in temperature, temperature change may affect the aye-aye's behavior indirectly through changes in environmental factors. In this connection, it is noteworthy that the aye-aye is more inclined to move by hanging from wire mesh as the temperature rises, a feat requiring a

considerable amount of energy. At night, when the aye-aye was generally active, sleeping, a component of resting, appeared to be unaffected by temperature changes, while sitting, another component constituting resting, decreased with rises in temperature. This suggests that the aye-aye is more active in summer than in winter.

2. Relative Distribution of Individual Activities and their Component Acts by Hour

The aye-aye's activity showed wide variation when analyzed by hour. The animal sometimes started to feed soon after sunset, while at other times, it was rather reluctant to feed at first and did not start feeding until 20:00 hrs.

The aye-aye's activity varied so widely from night to night that it would be as meaningless to follow the aye-aye's activity minutely night by night as it would compare a number of members with no regard to their individual differences. Nevertheless, when the aye-aye's activities are summed by hour and month, more or less consistent tendencies emerge.

Generally speaking, the aye-aye spent most of the time resting between 3:00 and 4:00 hrs. Feeding was high in the early and gradually fell toward the later at night. This pattern was common to all the months studied (Fig. 3).

Feeding, moving and "other activities" were combined as representing restlessness or "positive activity" of the aye-aye, and the proportional sum of these positive activities was calculated for each month. The proportion of positive activity was low, less than 50% from June/July to August. In contrast, the proportion of positive activity was high from September to November. In these months, however, the relative contributions of each individual activity constituting positive activity differed from each other.

3. Duration of Individual Component Acts

The aye-aye often took long rests during the night, its active period. This was conspicuous when the animal entered the nest box, where it habitually took rests lasting longer than 30 minutes and sometimes all through the early hours of the next morning. Similarly, in the case of moving, there were often instances exceeding 30 minutes in duration . However, such long durations were rather rare for other component acts.

In this paper, duration refers to the number of continuous samples recorded. Although acts consisting of a series of brief movements, such as tapping, the duration may be less than ten seconds, I would calculate its duration in the present method, when such acts repeated frequently .

I could easily determine seasonal changes in the duration of component acts. However, for resting and moving, the results are the same whether analyzed in terms of hourly proportion or their exact duration. Here, I analyzed seasonal changes in the duration of other component acts, such as eating, drinking, self-grooming, tapping and gnawing, which have comparatively short durations. The average bouts was calculated for each month and compared among the months studied (Table III).

(1) Eating

The average eating bout was longest in June/July and briefest in August. The longest bout occurred at 0 to 1 hrs on June 11 (102 sample lengths for eating an egg).

The average eating bout became relatively short after August, but did not show significant reduction thereafter.

(2) Drinking

The longest drinking bout was 14 sample lengths at 0:00 hrs on June 8th. The monthly average of drinking bouts was relatively high in June/July and

November, but low from August to October. The meaning of this pattern remains unclear.

(3) Self-grooming

The longest self-grooming bout was 29 sample lengths (at 0:00 to 1:59 hrs on July 17). The proportion of self-grooming was high in June/July and November, and low from August to October. However, the monthly averages of self-grooming bouts did not show comparable patterns of seasonal change, although significant differences were observed among the months studied.

(4)Tapping

The average bout of tapping was significantly longer in November than in any other month studied. This forms a characteristic feature of the aye-aye's activity in November together with the increased proportion of self-grooming at this period.

(5) Gnawing

Monthly changes in the average bout of gnawing were not clear as for tapping. The average bout of gnawing was rather constant regardless of the season. This act, once initiated, was continued for a certain stretch of time without interruption, in contrast to tapping.

4. Diet

(1) Food items and their relative intake

A total of 12 different food items, excluding coconuts water, were given to the aye-aye during the observation period (Table IV). Coconuts, bread, bananas, tomatoes, sugar cane and papayas were each served in an amount sufficient to meet the appetite of the aye-aye, so that a portion of them always left unconsumed the next morning. In contrast, the following food items were unlikely to be given in sufficient amounts: Eggs were usually served one per meal, and the yolk was completely consumed while the white was uneaten. If more than two eggs were served, more yolks would be consumed by

the aye-aye. This also holds true for ramy and honey. These foods were usually consumed completely, allowing to assume that amounts larger than provided would also have been consumed.

At the Tsimbazaza Zoo the aye-aye is given a variety of foods to maintain a good nutritional balance. Thus, the aye-aye was served three to seven different food items every night. Of all the food items served, the aye-aye spent the longest time (or the longest proportional eating time) on coconut, followed by ramy fruits, bread, bananas, etc. Coconut is the food item which was most easily obtainable during the observation period, and was most amply given of all the foods served.

Comparison of sample lengths of coconut eating to the total samples in which any feeding was registered (the relative coconut eating duration) revealed seasonal changes in coconuts eating, with decreases in coconut eating as temperature increased ($r=-0.837$, $p<0.05$).

Ramy nuts (Canarium madagascariense) were picked from trees planted on the grounds of the Tsimbazaza Zoo, and were served to the aye-aye from August, when the trees bear fruits, till November. The amount of ramy fruits given to the aye-aye was comparable to other food items. Proportional feeding on ramy was lowest in August, and leveled off from September to November.

Bread was often served soaked in sweetened condensed milk, and was consumed actively by the aye-aye. It was given as a staple food to the aye-aye. In contrast with coconut, it was more actively consumed with a rise in temperature ($r=0.934$, $p<0.05$). How a rise in temperature can affect the appetite of the aye-aye toward bread remains unclear.

Bananas were so avidly consumed by the aye-aye that in August, the feeding time on bananas was longer than on ramy fruits or on bread. After October, however, the proportional feeding time on bananas rapidly decreased.

This phenomenon may possibly be related to changes in preference toward bananas (or their status as a food), as seen for coconuts.

Usually, one egg was given per a meal. The little amount of the egg probably explains why the proportional feeding time for eggs was low compared to that for other food items. The skill with which the aye-aye consumes an egg demonstrates that the animal is well adapted to this food item.

Passion fruits and oranges were also presented to the aye-aye, but they were not eaten. In addition, the animal did not eat the leaves of tree-branches that were always placed in the feeding room to serve as nest material.

(2) Estimation of energy intake

The energy intake was calculated from the the ingested amount of foods (Table V). The energy intake averaged 306.1 kcal per meal (range=198.8-607.4, S.D.=107.46, n=16).

DISCUSSION

1. Nocturnal Activity

Studies on the nocturnal activity of the aye-aye have been very limited in number (Petter and Petter-Rousseaux, 1959; Petter, 1962; Winn, 1989). Furthermore, results based on quantitative measurement have never been presented. The present investigation can thus be viewed as a first step forward toward elucidation of the complete picture of the activity of the aye-aye.

However, this investigation suffers from a number of limitations: the study period was short, and depends upon a single adult female aye-aye secluded in a narrow space permitting only limited movement and feeding on a routine food menu.

Our major findings on the nocturnal activity of the aye-aye are as

follows.

The aye-aye is nocturnal and active any time at night, but from 2:00 hrs in the morning till just prior to dawn it often took a rest. In addition, at any time at night it returns to the nest to take a long rest (more than half an hour). 56.7 percent of its nocturnal activity was engaged in resting. Such proportion of the activities showed seasonal changes. Rises in atmospheric temperature were highly correlated with increases in the proportion of moving and hanging. Generally speaking, feeding was high in the early and gradually fell toward the later at night. The aye-aye was observed to engage in tapping and gnawing on any night during the period. These acts consist of a long series of gnawing at definite places on the window or the iron frame of the door.

2. Diets

I have reported on the diet of the aye-aye in the wild elsewhere (Iwano, in press, a). Here, I focus my attention on the feeding habits of the aye-aye in captivity.

Regarding feeding habits of the aye-aye under human care, Millot (1952) reviewed studies presented since its discovery. The food items the aye-aye has consumed under human care include bananas, mangoes, papayas, datepalms, coconuts, sugar cane, maze, insect larvae, eggs, honey, milk, boiled rice, vegetables, sugar water, grenadine syrup, and cafe au lait. Petter (1977) also confirmed that the captive aye-aye accepts a food menu such as that noted above.

The basic diet for the aye-ayes now kept in the Paris Zoo consists of coconuts, sugar cane, fruits (mango, avocado, orange, apple, date (Phoenix sp. ?), mealworms, protein-rich feed, cheese, and raw eggs; a diet which is practically the same as above (Winn, 1989). The aye-ayes in the Paris Zoo

were also given a wide variety of fruits (including fig, pear, etc.), vegetables (carrot, etc.) and nuts (Winn, 1989).

As is evident from inspection of the above food menus given to aye-ayes in captivity, the aye-aye can eat a wide variety of plants as well as animal-derived foods such as insects and bee honey, and they show a more or less individual variation (or more properly influenced by the feeding condition) in preference to such foods. Moreover, as is suggested from the result of my observations the aye-aye appears to select an appropriate menu according to the season.

Winn (1989) reported that the aye-ayes in the Paris Zoo do not eat tomatoes, but the aye-aye reported here ate tomatoes avidly. Shaw (1883) observed that the aye-aye did not eat honey or egg. This observation is contrary to the results of both my and other studies. According to Lamberton's observation (1934), some aye-ayes like sugar cane while others do not. My aye-aye actively ate sugar cane from July to September, but rarely ate it from October to November. Such within-species diet differences between local populations occur widely in other nonhuman primates (see review by Nishida, 1987).

4. Hard-nut Adaptation Hypothesis of the Aye-aye (Iwano and Iwakawa, 1988)

Winn (1989, p.114), based on the observation of an aye-aye's singular feeding behavior in which the aye-aye gnawed open the hard nut (stone) of a fruit, such as a peach to eat its content, supported our hypothesis (Iwano and Iwakawa, 1988).

Furthermore, taking a similar standpoint, she suggested that the feeding of the aye-aye on badamier nuts reported by Petter et al. (1977) could be better explained by consumption of their contents rather than searching for insect larvae hidden within the nuts. The belief in the aye-aye's preference

toward insect larvae is so deeply entrenched that Petter et al. (1977) might have been subject to this interpretational bias. In the same way, feeding by the aye-aye on the inside of the Afzelia bijuga bark at the Nosy Mangabe coast had been interpreted as a search for small living creatures inhabiting the bark (Pollock et al., 1985).

In corroboration of Winn's observation (1989), feeding on fruit stones was also confirmed for the aye-aye at the Tsimbazaza Zoo. After December, Mr. G. Rakotoarisoa gave plums to the aye-aye, which ate the endocarp as well as the mesocarp of the stone . The aye-aye apparently preferred endocarp to mesocarp, and tore open the stone by gnawing, to dig out its contents with the third digits.

5. Energy Intake

The aye-aye's average energy intake per meal 306 kcal. If the body weight of the aye-aye is assumed to be 2,695 g (based on data presented by Winn, 1989), the energy intake per 100g for a week corresponds to 79.5 kcal. The same kind of data has been presented by Petter-Rousseaux (1980) for various prosimian species. Comparing the present result reveals that the aye-aye's energy intake is close to that of Lepilemur ruficaudatus and substantially different from that of smaller prosimian groups (Table VI).

The proportion of feeding averaged about 14% of the total activity, equivalent to about 89 minutes in terms of total duration spent for feeding (this result is the same whether calculated from the duration of the total activity being 10.6 hours, or from 176.9 sample lengths, the average duration per night in which feeding was registered). This value lies within the upper limit of continuous stretches of feeding activity on ramy observed in the wild. If the aye-aye spent this same time for feeding on ramy at rate observed in the wild, it would consume 48.5 ramy fruits or ingest 212 kcal in

terms of energy. In contrast, the captive aye-aye's average energy intake per meal, as revealed in the present study, was 306 kcal. This figure is apparently higher than my estimation. In particular, even coconut has only 58% of the energy content of ramy, so energy intake over the same duration is expected to be less than the energy intake gained from consuming ramy alone.

The higher energy intake of the captive animal over its wild counterpart may be due to either of the following two factors: (1) overestimation of the energy intake of the captive animal (a portion of food may only have been torn and thrown away, and not consumed); and (2) increased feeding efficiency under human care in the zoo, allowing the aye-aye to consume a larger quantity of foods in the same interval, thus resulting in increased energy intake. Since zoo food is supplied in far more concentration than in the wild, the latter possibility would be a more important factor underlying the energy intake phenomenon.

The aye-aye's energy intake value, when presented as energy intake per meal, is not so much different from that of other prosimians, when allowance is made for difference in weight. Thus, the aye-aye in the wild may also ingest a comparable amount of energy with a similar commitment to feeding relative to total activity.

In macaques, the basal metabolic rate (BMR) is believed to be 49 kcal per 1kg weight (Benedict, 1938 quoted from Kleiber, 1975), and BMR for prosimians has been thought to be slightly less than that (Müller, 1985). Applying that the macaque's BMR to the aye-aye, gives 147 kcal as the BMR of an aye-aye weighing 3 kg. Thus, even 199 kcal, or the lowest energy intake ever observed in my aye-aye, would be sufficient to sustain the routine activity of the aye-aye, a member of another prosimian species.

6. Response of the Aye-aye to Light

The response of the aye-aye to light is markedly different from other

nocturnal prosimians. The aye-aye was not apparently disturbed when exposed to two intense lights each of 150 thousand lux (each being brighter than a car's front light) at a distance of about 2 m, not to mention the light of a torch. This holds true also for aye-ayes in the wild. Whereas other nocturnal prosimians become motionless when exposed to an intense light, aye-ayes, though sometimes being watchful of light and human existence, are not apparently disturbed by light.

This characteristic unresponsiveness of the aye-aye to light is quite noteworthy as a trait of a nocturnal animal (it is well known that even a diurnal animal strongly responds to intense light), and should be added to the list of its unique morphological traits as an unusual characteristic in the behavioral aspects or physiological responsiveness of this animal.

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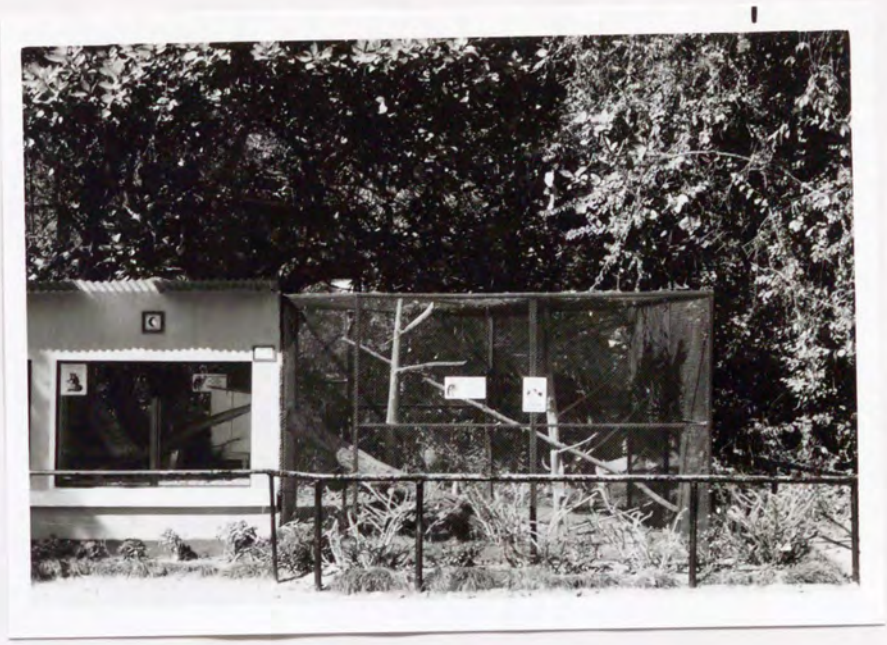

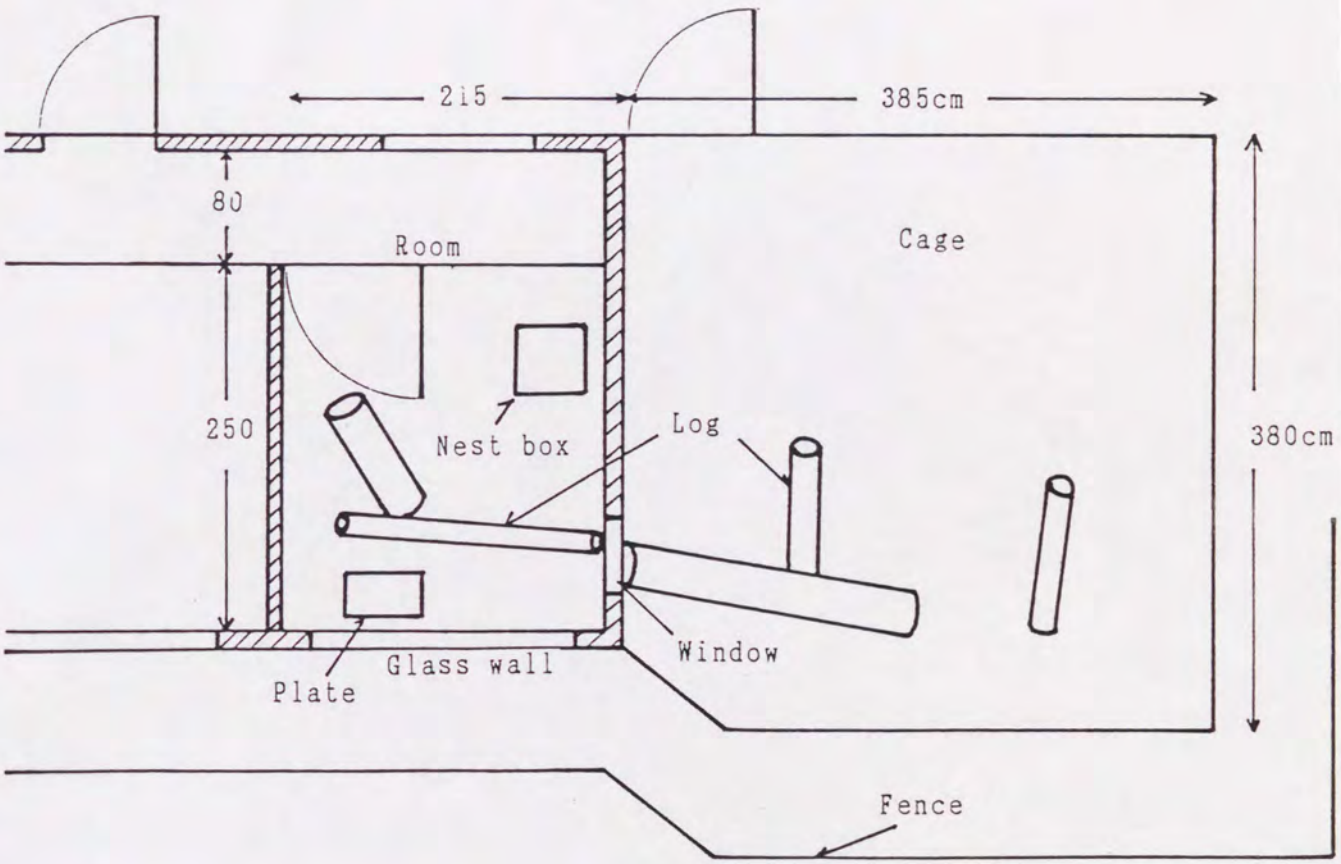

Fig. 1. Feeding facility of the aye-aye at the Tsimbazaza Zoo.

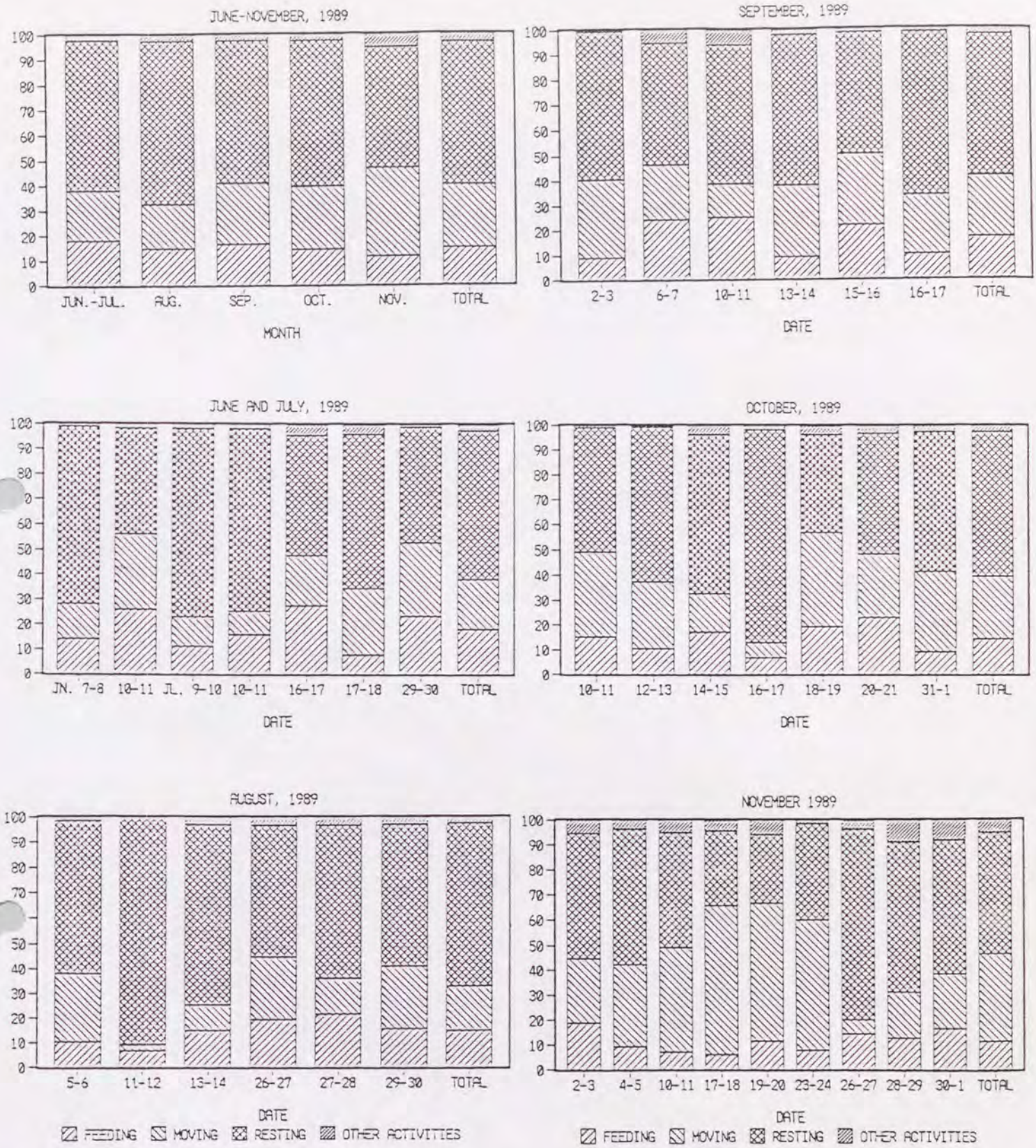

Fig. 2. Percentage of four activities for each night and month for the aye-aye at the Tsimbazaza Zoo in 1989.

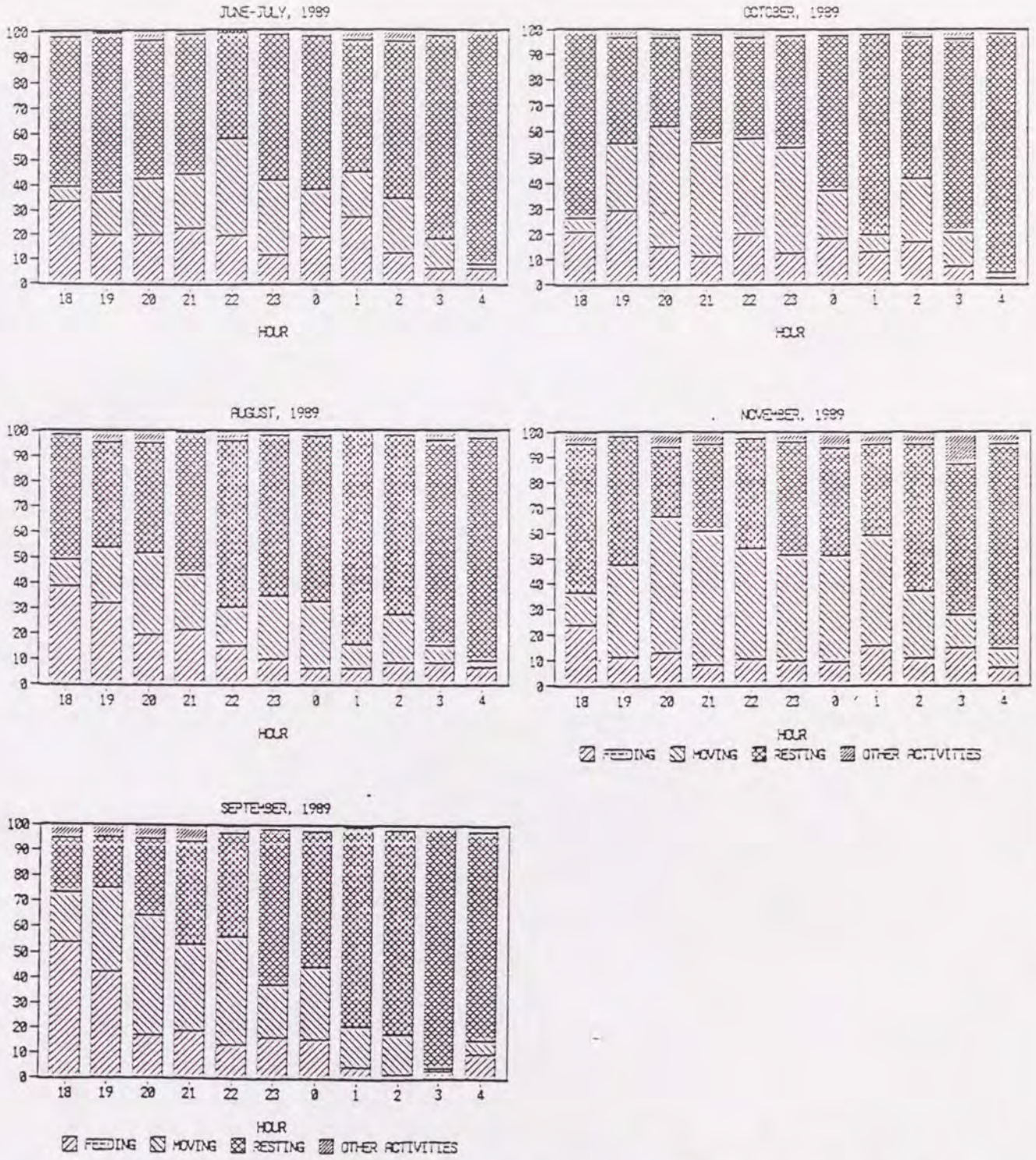

Fig. 3. Hourly patterns of feeding, moving, resting and other activities during the night for the aye-aye at the Tsimbazaza Zoo in 1989.

Table I Study period and observation samples on the activity of a captive aye-aye (*Daubentonia madagascariensis*) at the Tsimbazaza Zoo in 1989

	June/July	August	September	October	November	Total
Days	7	6	6	7	9	35
Hours	72	63	65	74	97	371
Hours/Day	10.3	10.5	10.8	10.6	10.8	10.6
Samples	8395	7335	7617	8736	11292	43375
Samples/Day	1199.3	1222.5	1269.5	1248.0	1254.7	1239.3

Table II Activity of the aye-aye in the Tsimbazaza Zoo between June and November, 1989 (Observaton samples)

	Month	June-July	August	September	October	November	Total
	Hour	72	63	65	74	97	371
	Sample No.	8395	7335	7617	8736	11292	43375
Place	Room	7098	6332	5893	6338	6276	31937
	Cage	1297	1003	1724	2398	5016	11438
Point	R.Ground	1719	1279	1329	1026	669	6022
	C.Ground	494	317	244	301	693	2049
	R.Tree	469	190	252	425	495	1831
	C.Tree	240	290	576	879	1993	3978
	On Nest	1221	1124	934	431	1133	4843
	Under Nest	234	22	241	0	23	520
	In Nest	3450	3527	2923	4274	3745	17919
	R.Wire Net	76	66	73	12	25	252
	C.Wire Net	439	385	904	1214	2330	5272
	R.Window	53	135	141	174	186	689
Acti-	Feeding	1522	1080	1258	1270	1300	6430
vity	Moving	1678	1290	1852	2193	3940	10953
	Resting	5002	4774	4286	5061	5463	24586
	Other	191	189	219	212	589	1400
	Total	8393	7333	7615	8736	11292	43369
Beha-	Eating	1456	1044	1223	1210	1260	6193
vior	Drinking	66	36	35	60	40	237
	Walking	1109	911	952	1059	1898	5929
	Climbing	178	19	2	66	238	503
	Hanging	279	332	873	970	1639	4093
	Jumping	112	29	25	115	165	446
	Standing	17	78	37	137	618	887
	Sitting	791	934	783	608	725	3841
	Self-grooming	308	164	120	55	307	954
	Sleeping	3886	3592	3299	4216	3708	18701
	Suspending	0	6	47	25	100	178
	R.Unknown	0	0	0	0	5	5
	Tapping	39	54	36	43	158	330
	Excretion	28	32	20	22	25	127
	Gnawing	112	97	127	121	270	727
	Smelling	7	5	15	4	12	43
	Licking	5	0	21	3	23	52
	Holding	0	0	0	2	0	2
	Pulling	0	0	0	20	91	111
	Playing	0	0	0	0	10	10
	Average Temperature (C)	13.3	13.6	15.0	17.9	19.3	

*: 6 activity samples are unknown.
C.: Cage
R.: Room

TABLE III Average bouts of eating, drinking, grooming, tapping and gnawing by the aye-aye in the Tsimbazaza Zoo between June and November, 1989.

Unit:30 seconds interval samples

Month		Eating	Drinking	Self-Grooming	Tapping	Gnawing
June-July	Ave.	10.55	5.50	2.68	1.39	2.55
	s.d.	12.30	4.37	3.43	0.82	1.88
August	Ave.	5.47	1.33	1.78	1.93	1.59
	s.d.	5.71	0.54	1.69	1.46	1.32
September	Ave.	6.27	1.40	2.73	1.50	2.08
	s.d.	5.79	0.80	3.99	0.65	1.88
October	Ave.	7.64	1.94	1.96	1.34	2.27
	s.d.	6.56	0.98	2.87	0.69	1.03
November	Ave.	6.89	2.22	1.88	2.14	1.89
	s.d.	6.62	0.79	1.68	1.67	1.37
Total	Ave.	7.36	2.21	2.21	1.66	2.08
	s.d.	1.95	0.46	0.46	0.42	0.33

Table IV Seasonal changes of food composition for the aye-aye in the Tsimbazaza Zoo between July and November, 1989 (Upper: Number of samples, Lower: Percentages)

Food	Month					Total
	July	August	September	October	November	
Coconut	627	446	421	367	236	2097
	67.9	41.3	33.5	28.9	18.2	36.0
Ramy	-	162	307	284	285	1038
	-	15.0	24.4	22.4	21.9	17.8
Bread	53	113	207	230	333	936
	5.7	10.5	16.5	18.1	25.6	16.0
Banana	49	211	186	27	-	473
	5.3	19.5	14.8	2.1	-	8.1
Honey	-	-	61	170	147	378
	-	-	4.8	13.4	11.3	6.5
Egg	15	55	30	44	160	304
	1.6	5.1	2.4	3.5	12.3	5.2
Tomato	-	38	11	64	48	161
	-	3.5	0.9	5.0	3.7	2.8
Sugar cane	124	-	2	23	-	149
	13.4	-	0.2	1.8	-	2.6
Papaya	21	11	2	-	26	60
	2.3	1.0	0.2	-	2.0	1.0
Palm fruit	-	-	-	-	25	25
	-	-	-	-	1.9	0.4
Milk	-	1	6	-	-	7
	-	0.1	0.5	-	-	0.1
Pineapple	-	-	2	-	-	2
	-	-	0.2	-	-	0.0
Coconut water	1	34	23	47	30	135
	0.1	3.1	1.8	3.7	2.3	2.3
Water	-	-	-	13	10	23
	-	-	-	1.0	0.8	0.4
Unidentified	34	9	-	1	-	44
	3.7	0.8	-	0.1	-	0.8
Total	924	1080	1258	1270	1300	5832
	100.0	100.0	100.0	100.0	100.0	100.0

-: In these months these foods did not given.

Table V Weights and energies of foods eaten by the aye-aye in the Tsimbazaza Zoo between September and November, 1989
(Upper:Weight(g), Lower:Energy(Kcal))

Date	Food items												Total energy (Kcal)
	CO.	RA.	BR.	BA.	HO.	EGG	TO.	SU.	PA.	AV.	MA.	C.W.	
Sep.16	40	-	10	35	+	20	-	-	-	-	-	-	
	136		31	31	+	74							272
Oct.24	50	-	30	10	50	-	65	-	-	-	-	-	
	170		93	9	147		10						429
25	10	-	30	30	-	35	-	-	-	-	-	-	
	34		93	26		82							235
26	10	-	30	-	27	35	20	-	-	-	-	-	
	34		93		79	82	3						291
27	-	-	40	-	-	30	-	-	-	10	10	75	
			124			75				30	7	11	247
28	-	-	35	-	36	-	80	-	50	-	-	-	
			109		106		13		25				253
29	-	5	30	30	-	10	10	-	50	-	-	-	
		31	93	26		37	2		25				214
30	-	-	30	-	36	-	60	-	60	-	-	-	
			93		106		10		29				238
31	-	-	50	-	-	10	10	30	-	-	-	-	
			155			37	2	78					272
Nov. 1	-	-	30	-	36	-	-	-	-	-	-	-	
			93		106								199
2	20	14	40	-	-	20	-	-	-	-	-	140	
	68	83	124			74						20	369
3	20	-	20	-	60	-	10	-	30	-	-	-	
	68		62		176		2		15				323
4	20	-	150	-	-	20	-	-	-	-	-	-	
	68		465			74							607
5	10	-	30	-	36	-	40	-	-	-	-	-	
	34		93		106		6						239
6	30	-	50	-	60	-	50	-	-	-	-	-	
	102		155		176		8						441
9	20	5	40	-	-	-	-	-	80	-	-	100	
	68	26	124						39			14	271

Abbreviation of food items, latin names and their energies

		(kcal/100g)
CO.	Coconut (*Cocos nucifera* L.)	340
RA.	Ramy (*Cananium madagascariense* Engle.)	584
BR.	Bread with milk	310
BA.	Banana (*Musa sapientum* L.)	87
HO.	Honey	294
EGG	Egg	372
TO.	Tomato (*Lycopersicon esculentum* Mill.)	16
SU.	Sugar cane (*Saccharium officinanum* L.)	259
PA.	Papaya (*Carica papaya* L.)	49
AV.	Avocado (*Persea amerinana* Mill.)	191
MA.	Mango (*Mangifera indica* L.)	68
C.W.	Coconuts water	14

Table VI Comparison of body weights and energy intakes for six Malagasy prosimians species

Species	Weight g	Energy intake Kcal/100g, 7day	Reference
Microcebus murinus	65	115	Petter-Rousseaux, 1980
M. coquereli	300	140	Petter-Rousseaux, 1980
Cheirogaleus medius	200	86	Petter-Rousseaux, 1980
Phaner furcifer	300	99	Petter-Rousseaux, 1980
Lepilemur ruficaudatus	500 - 900	71	Petter-Rousseaux, 1980
Daubentonia madagascariensis	2695	-	Winn, 1989
	-	80	Present study